

Weed species and traits associated with organic grain crop rotations in the mid-Atlantic region

John R. Teasdale¹ , Steven B. Mirsky² and Michel A. Cavigelli³

Research Article

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Author for correspondence:

John Teasdale, USDA-ARS, Building 001, Room 245, 10300 Baltimore Avenue, Beltsville, MD 20705. Email: john.teasdale@ars.usda.gov

¹Biological Collaborator, Sustainable Agricultural Systems Lab, Agricultural Research Service, U.S. Department of Agriculture, Beltsville, MD, USA; ²Research Ecologist, Sustainable Agricultural Systems Lab, Agricultural Research Service, U.S. Department of Agriculture, Beltsville, MD, USA and ³Research Soil Scientist, Sustainable Agricultural Systems Lab, Agricultural Research Service, U.S. Department of Agriculture, Beltsville, MD, USA

Abstract

Organic cropping systems are characterized by soil-disturbance events that can be diversified over years through crop rotations and within seasons by varying planting dates. The Farming Systems Project at Beltsville, MD, USA, is a long-term experiment that includes three organic rotations, corn (*Zea mays* L.)–soybean [*Glycine max* (L.) Merr.], corn–soybean–wheat (*Triticum aestivum* L.), and corn–soybean–wheat–alfalfa (*Medicago sativa* L.). Analysis of weed presence and cover over the first 18 yr of this experiment revealed that the tall, erect annual broadleaf weeds smooth pigweed (*Amaranthus hybridus* L.), common lambsquarters (*Chenopodium album* L.), horseweed (*Erigeron canadensis* L.), jimsonweed (*Datura stramonium* L.), and/or velvetleaf (*Abutilon theophrasti* Medik.) were most prominent in corn and soybean. Generally, these species exhibited traits adapted to the disturbance regimes, nutrient availability, crop environment and duration, and local meteorological conditions associated with the summer annual corn and soybean crops. Abundance of *A. hybridus*, *D. stramonium*, and *A. theophrasti* were controlled primarily by rotation diversity, whereby presence and cover of these species were highest in the short corn–soybean rotation and lowest in the longer rotations that had more diverse seasonal soil-disturbance regimes. Early-season temperature was the primary factor controlling *C. album* presence and cover, which were higher at lower temperatures associated with earlier planting dates. Higher early-season precipitation was the primary factor associated with higher presence of annual grass species. The relative abundance of species in organic corn and soybean was determined primarily by the diversity of crops and disturbance operations in rotation, the timing of spring tillage and planting, and annual meteorological conditions driving emergence periodicity.

Introduction

Cropping operations simplify ecosystem diversity by supporting primarily plant species that provide economic returns and/or ecological services. Consequently, it is not surprising that the weed species that often survive in this environment are those with traits that allow them to establish and reproduce similarly to crop plants, that is, they mimic the traits of their associated crops (Fried et al. 2008). This process of selection has been characterized using the analogy of filters that remove species with incompatible traits and allow species with traits compatible with system management operations and local meteorological conditions (Booth and Swanton 2002). From this perspective, the behavior of weed species in organic cropping systems can be understood in terms of the traits that are filtered by key factors operating in these systems (Ryan et al. 2010; Storkey et al. 2010).

Soil disturbance by mechanical tillage is a fundamental operation in organic cropping systems for removal of weeds both preplanting to prepare a seedbed and postplanting to eliminate weed competition. Although research has explored the potential for organic production without tillage (Wallace et al. 2018), most organic farmers rely on tillage as a primary tool for managing weeds (Baker and Mohler 2015; DeDecker et al. 2014). Soil disturbance is an important filter that defines the assembly of plant communities (Cordeau et al. 2017; Dinnage 2009). Specifically, the season of disturbance has a major influence on filtering the plant community (Crawley 2004; Fried et al. 2008; Smith 2006), whereby spring tillage favors summer annual species and fall tillage favors winter annual and perennial species. The timing of tillage operations across a region has been shown to act primarily on traits, rather than on specific species per se (Cordeau et al. 2017). Bernstein et al. (2014) suggested that annual spring tillage would impose greater competitive pressure on summer annual crops by promoting summer annual weed species (presumably possessing traits similar to their associated summer annual crops).

Crop rotation has been identified as an important management tool used by organic farmers for controlling weeds (Baker and Mohler 2015; DeDecker et al. 2014). The diversification of crops in rotations can reduce the abundance of dominant species and increase species diversity and evenness, and the associated diversification of seasonal tillage operations undoubtedly plays

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an important role in this effect (Teasdale 2018). Fried et al. (2008) suggest that a complex rotation with a complex array of crop rotations would aid weed control by dampening populations of dominant noxious species and would be more favorable to species adapted to a range of cropping conditions, resulting in weed communities rich in generalist species. Mohler et al. (2018) showed that vegetable crop rotations that employ multiple, appropriately timed tillage operations deplete the seedbanks of weed species having full-season reproductive requirements in favor of species with shorter reproductive cycles.

Long-term cropping-system experiments are useful for assessing weed species dynamics and identifying filtering factors and functional traits that permit weed adaptation (Ryan et al. 2010). The Farming Systems Project (FSP) at Beltsville, MD, was designed to understand ecological processes underlying crop performance in mid-Atlantic conventional and organic cropping systems. This long-term experiment includes a comparison of organic cropping systems that differ in rotational length and crop diversity, including combinations of summer annual, winter annual, and perennial crops. Recent reports have summarized annual corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] grain yields (Teasdale and Cavigelli 2017) and total weed abundance (Teasdale et al. 2018) over the first 18 yr of this experiment. Meteorological and crop operational variables were identified that influenced total weed abundance, both directly and through indirect influences on crop performance, which in turn influenced weeds. The season of tillage as dictated by crop rotation and the timing of tillage within a season also were important variables influencing weed performance. Because the timing of tillage has an important effect on the meteorological and environmental conditions that weed seeds will encounter during germination and emergence (Facelli et al. 2005), tillage timing is expected to be an important filter for determining the dynamics of the major weed species and their traits at FSP. Consequently, in contrast with the previous paper, which focused on total weed cover (Teasdale et al. 2018), this paper focuses on the behavior of the major species that contributed to the total weed cover in FSP organic crop rotations during the first 18 yr of this experiment. The objectives were (1) to define management factors in three organic grain crop rotations and the fluctuating annual conditions that influenced the presence and abundance of the dominant weed species, and (2) to identify traits that allowed the dominant species to persist in these organic rotations.

Materials and Methods

The FSP was conducted at the USDA-ARS Beltsville Agricultural Research Center in Beltsville, MD. Details of this experiment and reports on crop yield and total weed abundance are described in Teasdale and Cavigelli (2017) and Teasdale et al. (2018). This paper will report on responses of the major weed species in three organic systems differing in rotational diversity. The three organic rotations were (1) a 2-yr corn-soybean rotation (Org2) (2) a 3-yr corn-soybean-wheat (*Triticum aestivum* L.) rotation (Org3), and (3) a 6-yr corn-soybean-wheat-alfalfa (*Medicago sativa* L.) rotation (Org6). The longest rotation was initially a 4-yr rotation during the first 4 yr of the experiment with orchardgrass (*Dactylis glomerata* L.) and red clover (*Trifolium pratense* L.) as a 1-yr forage crop, but was expanded to 6 yr thereafter with 3 yr of alfalfa as the forage crop. A cereal rye (*Secale cereale* L.) cover crop was planted following corn in all rotations, and a winter annual legume cover crop was planted the fall before corn in Org2 and Org3. The

experiment was arranged in a split-plot design, with crop rotation as the main plot and crop phase as the subplot. All rotational crop phases were present in each year of the experiment. Corn and soybean were the only crops present in all rotational systems in every year, so weed assessments are reported from these crops only. The rotational treatments were arranged in a randomized complete block design with four replications. Each crop within a rotation was planted into a subplot that was 9.1-m wide (12 corn or soybean rows) and 111-m long.

Weed Cover Ratings

The percentage of soil area covered by weeds (weed cover) was estimated visually by the same rater in all years at crop maturity within the middle six rows of four 28-m-long quadrants of each corn and soybean subplot. Thus, a 4.6 m by 28 m quadrant was the experimental unit for this data set. Estimates included total weed cover and the percent contribution of major species in each quadrant. Cover ratings were primarily focused on the prominent species observed in each quadrant and were not intended to give a complete catalogue of every species present. Any species that did not make up at least 1% of the total cover present usually was not recorded. Consequently, this database is not adequate for conducting a complete community analysis of species, but is more suited to describing the dynamics of the most prominent species. Additionally, the number of species that occurred was relatively small, further reinforcing the focus on individual species.

Cycle Characterization

The first 18 yr of this experiment included three cycles of the 6-yr organic rotation. Each cycle of the 6-yr rotation included three cycles of the 2-yr rotation and two cycles of the 3-yr rotation. Therefore, the three 6-yr rotation cycles included a complete number of cycles of each rotation in this experiment. Organizing the analyses and presentation of results around the three 6-yr rotational cycles (Cycle 1 = 1997 to 2002, Cycle 2 = 2003 to 2008, and Cycle 3 = 2009 to 2014) proved to be a convenient way to demonstrate the overall trends in this data set. In addition, the three cycles coincided with overall management and weed species shifts that had definitive impacts on weed species behavior. Cycle 1 was characterized by no/minimum tillage before row crops, whereas plow tillage was initiated in 2003 at the beginning of Cycle 2 and continued thereafter. Cycle 3 was characterized by the rapid invasion of primarily jimsonweed (*Datura stramonium* L.) and velvetleaf (*Abutilon theophrasti* Medik.) into the experiment.

Analyses

The differences in species frequency observed in the three cycles of this experiment (to be described later) dictated that analyses of rotational treatments be conducted separately for each cycle. Each of the most frequently observed species in each cycle were analyzed for rotational treatment effects. The cover data for all species other than smooth pigweed (*Amaranthus hybridus* L.) had zero values in a substantial number of quadrants, and, where present, the data generally displayed a high degree of skewness and kurtosis. As a result, analyses were done in two phases, one analysis determined the presence and absence of a species, and the second analyzed species cover using a nonnormal distribution for quadrants where that species was present.

First, the binary data set of presence or absence for each of the most prominent species in each cycle was analyzed with a

generalized linear mixed model (PROC GLIMMIX, SAS v. 9.3, SAS Institute, Cary, NC) with a binary distribution and a logit link function. Model fixed effects were experimental rotation and crop, while year and block were random effects. Crop effects were not a focus of this analysis, but crop did represent a fixed effect that accounted for significant variation in many cases and improved the precision of analyses. Second, a data set of cover values in quadrants where a species was present was assembled for each species, and each data set was analyzed within each cycle with a generalized linear mixed model (PROC GLIMMIX) with a negative binomial distribution and a log link function. This analytical approach did not give convergence in many cases using a full set of fixed and random effects based on the experimental design, but a simplified model with experimental rotation as fixed effect and year as random effect provided a solution in most cases.

Amaranthus hybridus, common lambsquarters (*Chenopodium album* L.), and annual grasses were the species most consistently present and with the highest cover ratings during the 12-yr period of Cycles 1 and 2. Consequently, an assessment of the meteorological and management factors most highly associated with presence and cover of these species was undertaken using correlation and regression analyses. Cycle 3 was not included in these analyses because of the confounding presence of *D. stramonium* and *A. theophrasti* as they progressively invaded quadrants during this cycle. A binary data set was constructed consisting of the absence or presence of each species (values of 0 or 1, respectively) in all quadrants. Quantitative levels of the following management factors were developed. Rotation levels were defined by the number of years without a row crop before corn (equal to 0 for Org2, 1 for the Org3, and 2 to 4 for Org6 depending on the duration of the forage crop). Primary tillage levels were 0 for no-till planting into cover crops that were mowed, rolled, or skim disked; 1 for seedbed preparation with a chisel plow and disk; and 2 for seedbed preparation with a moldboard plow and disk. Primary tillage level was highly confounded with rotary hoeing and sweep cultivation frequency, so rotary hoe and cultivation variables were not included. Planting date were quantitated as the number of days after April 30. Average daily temperature and total precipitation were computed for each week after planting. Weed presence was correlated to weekly temperature and precipitation values, and consecutive 4- to 5-wk periods were chosen before and after planting that provided the highest correlation, using a process similar to previous analyses of meteorological influences on crop yield (Teasdale and Cavigelli 2017) and total weed cover (Teasdale et al. 2018). Pearson correlation coefficients were determined among all variables in the data set (PROC CORR, SAS v. 9.3). Logistic regression was conducted with weed binary values as a function of management, temperature, and precipitation variables using a logit link function and a stepwise selection process, with $P < 0.01$ as the criterion for entry and retention in the model (PROC LOGISTIC, SAS v. 9.3). Probability was modeled for the presence of each weed species (binary value = 1). Because planting date was highly correlated with temperature ($r = 0.71$ to 0.84) and precipitation ($r = 0.50$ to 0.56), planting date was either not included when meteorological variables were included, or meteorological variables were not included when planting date was included. Standardized regression coefficients were computed to assess the relative importance of each variable retained in the model. The R^2 value, adjusted to a maximum value of 1, assessed the capacity of independent variables to predict the binary data set.

A second set of analyses were conducted on the response of weed cover values to explanatory variables using a database created

for each weed that included only quadrants where cover > 0 . These data sets included the logit of weed cover as well as explanatory variables for those quadrants. The logit transformation of weed cover values provided the best fit to a normal distribution. The same management variables were used as in the preceding analysis. Meteorological variables were derived by a process similar to that described in the preceding analysis, but in this case included ranges of consecutive weeks in early season and in midseason that provided the highest correlation with the logit of weed cover. In addition, two variables defining potential competition from the crop and other weeds were introduced. Potential crop competition was defined by crop yield (standardized separately for corn and soybean to units with a mean = 0 and an SD = 1), as described in Teasdale et al. (2018). Potential competition from other weeds in a quadrant was defined by the logit of weed cover of all other weeds (equal to total weed cover minus the weed cover of the species being analyzed). Multiple regression of the logit of weed cover for *A. hybridus*, *C. album*, or annual grasses in response to competition, management, and meteorological variables was determined by least-squares estimation procedure using stepwise selection with entry and retention at $P < 0.01$ (PROC REG, SAS v. 9.3).

Analyses were conducted on the rate of *D. stramonium* and *A. theophrasti* cover increase in quadrants invaded by these species. Because *D. stramonium* and *A. theophrasti* were considered invaders into the experimental area, it was expected that the magnitude of their cover would be affected by the number of years that the population had to multiply after the initial invasion of a particular quadrant. Consequently, a data set for each species was created that included only the year of first appearance and all subsequent years. Accordingly, a new variable was created named “progression year,” where 1 equaled the year the weed was first observed in a quadrant and 2, 3, . . . designated the successive years following the invasion year. These data sets allowed more precise determination of differences in the rate of cover development between crop rotations based on comparable time periods following invasion. Homogeneity of slope tests using analysis of covariance were conducted on the logits of *D. stramonium* and *A. theophrasti* cover as a function of progression year. Because there were no significant differences among rotations in cover values in the first year of invasion, this analysis was conducted with a common intercept, a regression coefficient for the slope of weed cover per progression year, and a coefficient for the interaction of slope and rotation. A mixed model was employed, with rotation as a fixed effect and block as a random effect (PROC MIXED, SAS v. 9.3). Preliminary analyses demonstrated that regressions were linear in most cases, so all homogeneity of slope tests were performed on linear models only.

Results and Discussion

Eight species or species groups were present in at least 5% of quadrants and will be the focus of this investigation. Their frequency of occurrence by cycle is presented in Table 1. In addition, 12 weed species—Virginia copperleaf (*Acalypha virginica* L.), common ragweed (*Ambrosia artemisiifolia* L.), mugwort (*Artemisia vulgaris* L.), Canada thistle [*Cirsium arvense* (L.) Scop.], smallflower galinsoga (*Galinsoga parviflora* Cav.), prickly lettuce (*Lactuca serriola* L.), common pokeweed (*Phytolacca americana* L.), curly dock (*Rumex crispus* L.), prickly sida (*Sida spinosa* L.), horsenettle (*Solanum carolinense* L.), eastern black nightshade (*Solanum ptychanthum* Dunal), and dandelion (*Taraxacum officinale*

Table 1. Frequency of occurrence of the most common weed species in corn and soybean quadrants during three rotation cycles at the Farming Systems Project, Beltsville, MD.

Weed species	Common name	Bayer code	Frequency of occurrence in		
			Cycle 1 (1997–2002)	Cycle 2 (2003–2008)	Cycle 3 (2009–2014)
			%		
<i>Amaranthus hybridus</i> L.	Smooth pigweed	AMACH	87	94	92
<i>Chenopodium album</i> L.	Common lambsquarters	CHEAL	86	47	58
-	Annual grass species ^a	Anngr	46	59	64
<i>Erigeron canadensis</i> L.	Horseweed	ERICA	50 ^b	0	0
<i>Persicaria</i> sp.	Smartweed species ^a	POLsp	15	2	1
<i>Ipomoea</i> sp.	Morningglory species ^a	IPOsp	1	9	47
<i>Datura stramonium</i> L.	Jimsonweed	DATST	0	5	51
<i>Abutilon theophrasti</i> Medik.	Velvetleaf	ABUTH	0	1	20

^aAnnual grass species were primarily giant foxtail (*Setaria faberi* Herrm.), fall panicum (*Panicum dichotomiflorum* Michx.), and barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.] in Org2 and Org3; and large crabgrass [*Digitaria sanguinalis* (L.) Scop.] and yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult.] in Org6. Morningglory species were primarily ivyleaf (*Ipomoea hederacea* Jacq.) and tall morningglory [*Ipomoea purpurea* (L.) Roth]. Smartweed species were primarily Pennsylvania smartweed [*Persicaria pensylvanica* (L.) M. Gomez] and ladysthumb (*Persicaria maculosa* Gray).

^bThis species occurred only at the indicated frequency in Cycle 1 soybean, it did not occur in Cycle 1 corn or in Cycles 2 or 3.

F. H. Wigg.)—and two volunteer forage species—alfalfa and orchardgrass—were recorded in less than 2% of quadrants. Many of these infrequently occurring species were carryovers from the several years of conventional no-till corn and alfalfa that had been grown on this site before the FSP experiment, and they will not be discussed further.

Cycle Effects

The frequency of *A. hybridus* occurrence was 87% to 94% in all cycles (Table 1). Annual grass appeared in approximately one-half to two-thirds of quadrants across all cycles. *Chenopodium album* occurrence was 86% in Cycle 1, similar to that of *A. hybridus*, but it declined in Cycles 2 and 3. This decrease in *C. album* occurrence is clearly aligned with the increase in tillage from Cycle 1 to Cycles 2 and 3 and will be discussed later in this report. The patterns of *E. canadensis* and *Persicaria* sp. occurrence also were influenced by the increase in tillage after Cycle 1 and will be discussed here.

Erigeron canadensis

This species demonstrated a remarkable pattern of presence and absence, wherein it was only present in Cycle 1 soybean, but was completely absent from any quadrant in Cycles 2 or 3 and from any Cycle 1 corn quadrant (Table 1). The presence and absence of tillage defined this pattern. The rye cover crop was mowed in 2000 to 2002, and soybean was planted without tillage into this residue. *Erigeron canadensis*, which typically emerges in either fall or early spring (Weaver 2001), established in the rye cover crop and survived the mowing operation. In contrast, a hairy vetch (*Vicia villosa* Roth) cover crop was rolled in 2000 to 2002 Org2 and Org3 corn, and growth of this cover crop was sufficiently dense to smother emerging *E. canadensis* seedlings. The forage crop was plowed before Org6 corn in these years, which destroyed emerged *E. canadensis* seedlings. Before 2000, cover crops were disked before planting corn and soybean, which also destroyed *E. canadensis* seedlings. All corn rotations were moldboard plowed, and all soybean rotations were chisel plowed and disked after 2002, accounting for the absence of *E. canadensis* in all Cycle 2 and 3 quadrants. The relative lack of dormancy of this species and its relatively high seed mortality rate in soil (Weaver 2001)

also account for the rapid elimination of this species after an annual spring tillage regime was initiated.

Persicaria species

The frequency of *Persicaria* sp. was higher in Cycle 1 than in subsequent cycles (Table 1). *Persicaria* sp. emerge relatively early in spring with a short emergence duration (Werle et al. 2014), and growth of these weeds is promoted by wet soil conditions (Pickett and Bazzaz 1976). The reduced-tillage conditions of Cycle 1 would favor weeds emerging in cooler, wetter soil conditions, whereas the more intensive tillage operations in Cycles 2 and 3 occurred later in the spring, when soils became sufficiently dry (planting dates were on average 9 and 12 d later in Cycles 2 and 3, respectively, than in Cycle 1), and would have been less favorable for establishment of these species.

Species with Increased Presence in Cycle 3

The presence of *D. stramonium*, *A. theophrasti*, and *Ipomoea* sp. in organic quadrants increased in Cycle 3 (Table 1). *Ipomoea* sp. were present intermittently throughout the experiment, but were at a relatively low frequency until 2009, when their presence increased. In contrast, *D. stramonium* and *A. theophrasti* were almost absent from the experiment until their appearance in 2006 to 2007, after which their occurrence increased substantially. In addition, these three species first appeared and increased in the same quadrants at the same time. The location of quadrants where these species initially appeared was at the end of the field closest to the gate. This suggests that these species may have been introduced into these quadrants on farm equipment. They progressively appeared in all blocks of the field, suggesting continued dispersion by farm equipment in subsequent years.

Rotation Effects

The total weed cover in each cycle confirmed results presented earlier (Teasdale et al. 2018), whereby highest total weed cover was found in the Org2 rotation (Tables 2–4). The Org3 rotation reduced total weed cover in two of three cycles, and the Org6 rotation reduced total weed cover in all three cycles compared with Org2. These decreases have been explained by the interruption of weed life cycles as the rotations increased in length and included

Table 2. Probability that weed species occurred in quadrants of three organic rotations at the Farming Systems Project, Beltsville, MD, during Cycle 1 (1997–2002).^a

Species	Rotation ^b	Probability of occurrence	Soil cover when present
		%	
AMACH	Org2	98.2 a	19.6 a
	Org3	95.1 b	8.5 b
	Org6	86.0 c	9.8 b
CHEAL	Org2	93.9 a	23.4 a
	Org3	89.3 a	11.2 b
	Org6	95.3 a	19.1 a
Anngr	Org2	30.7 b	12.4 a
	Org3	64.4 a	9.5 a
	Org6	42.5 b	8.9 a
ERICA ^c	Org2	86.0 ab	19.7 a
	Org3	71.0 b	10.5 b
	Org6	94.0 a	7.5 b
POLsp	Org2	6.4 b	5.5 a
	Org3	12.6 a	4.7 a
	Org6	2.5 c	2.6 a
Total ^d	Org2	100	55.2 a
	Org3	100	32.4 c
	Org6	99.1	39.2 b

^aValues are least-squares means back-transformed from a logit link function. Also shown is soil coverage for quadrants where each species occurred. Cover data are least-squares means back-transformed from a log link function. Values followed by the same letter within species are not significantly different ($P < 0.05$).

^bOrg2, 2-yr corn–soybean rotation; Org3, 3-yr corn–soybean–wheat rotation; Org6, 6-yr corn–soybean–wheat–forage rotation (included an orchardgrass/red clover forage crop during the first 4 yr of this cycle, but an alfalfa forage crop during the remainder of the cycle).

^cThis species was only present at the indicated probabilities in soybean from 2000 to 2002.

^dTotal also includes minor species not listed in this table.

Table 3. Probability that weed species occurred in quadrants of three organic rotations at the Farming Systems Project, Beltsville, MD, during Cycle 2 (2003–2008).^a

Species	Rotation ^b	Probability of occurrence	Soil cover when present
		%	
AMACH	Org2	100	21.5 a
	Org3	99.8 a	23.1 a
	Org6	93.1 b	9.2 b
CHEAL	Org2	19.8 c	2.9 b
	Org3	29.3 b	1.7 c
	Org6	71.6 a	5.1 a
Anngr	Org2	76.7 a	11.7 a
	Org3	52.2 b	9.6 a
	Org6	82.1 a	12.5 a
Total ^c	Org2	100	33.9 a
	Org3	100	30.2 a
	Org6	97.3	21.1 b

^aValues are least-squares means back-transformed from a logit link function. Also shown is soil coverage for quadrants where each species occurred. Cover data are least-squares means back-transformed from a log link function. Values followed by the same letter within species are not significantly different ($P < 0.05$).

^bOrg2, 2-yr corn–soybean rotation; Org3, 3-yr corn–soybean–wheat rotation; Org6, 6-yr corn–soybean–wheat–alfalfa rotation.

^cTotal also includes minor species not listed in this table.

more phenologically diverse crops (Teasdale 2018; Teasdale et al. 2004). Several weed species responded similarly to rotations and were primarily responsible for the total weed cover response. *Amaranthus hybridus* was the most frequently encountered species in this experiment, and cover was reduced by approximately one-half in Org6 compared with Org2 in every cycle. *Erigeron*

Table 4. Probability that weed species occurred in quadrants of three organic rotations at the Farming Systems Project, Beltsville, MD, during Cycle 3 (2009–2014).^a

Species	Rotation ^b	Probability of occurrence	Soil cover when present
		%	
AMACH	Org2	98.8 ab	17.7 a
	Org3	99.5 a	15.0 a
	Org6	98.3 b	8.1 b
CHEAL	Org2	33.7 c	4.5 b
	Org3	64.4 b	9.4 a
	Org6	81.9 a	6.7 ab
Anngr	Org2	55.0 b	2.5 b
	Org3	53.0 b	1.1 c
	Org6	85.7 a	6.4 a
IPOsp	Org2	65.2 a	3.1 a
	Org3	53.8 b	1.0 b
	Org6	16.7 c	1.3 b
DATST	Org2	84.4 a	12.9 a
	Org3	61.5 b	4.3 b
	Org6	9.3 c	3.3 c
ABUTH	Org2	22.1 a	11.1 a
	Org3	22.9 a	5.8 a ^c
	Org6	2.4 b	6.1 a ^c
Total ^d	Org2	99.4	38.5 a
	Org3	100	26.0 b
	Org6	100	19.3 c

^aValues are least-squares means back-transformed from a logit link function. Also shown is soil coverage for quadrants where each species occurred. Cover data are least-squares means back-transformed from a log link function. Values followed by the same letter within species are not significantly different ($P < 0.05$).

^bOrg2, 2-yr corn–soybean rotation; Org3, 3-yr corn–soybean–wheat rotation; Org6 = 6-yr corn–soybean–wheat–alfalfa rotation.

^cValues were significantly different from Org2 value at $P < 0.10$, but not at $P < 0.05$.

^dTotal also includes minor species not listed in this table.

canadensis, during its limited appearance in Cycle 1, also exhibited higher weed cover in Org2 than in Org3 and Org6. In Cycle 3, *D. stramonium*, *A. theophrasti*, and *Ipomoea* sp. responded both with higher presence and/or higher cover in Org2 than in Org3 and Org6.

Chenopodium album had a mixed response to rotations (Tables 2–4). In Cycle 1, where it was the codominant species along with *A. hybridus*, it reduced cover in Org3 relative to Org2. In Cycles 2 and 3, this species became a relatively minor species compared with *A. hybridus* and made little contribution to total cover. However, in all cycles, this species had similar or higher frequency and cover in Org6 than Org2, a result that will be discussed further below.

Annual grasses were not the most dominant species but were consistent constituents of the weed community in all cycles and rotations and exhibited minimal differences among rotations (Tables 2–4). The grass species' constituents of rotations were distinct, in that Org2 and Org3 were dominated by the more upright species fall panicum (*Panicum dichotomiflorum* Michx.), giant foxtail (*Setaria faberi* Herrm.), and barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.], whereas Org6 was dominated by the more prostrate species large crabgrass [*Digitaria sanguinalis* (L.) Scop.] and yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult.]. This has been explained previously by the selection imposed by mowing in the rotation including forage crops (Teasdale et al. 2004). Weed presence and cover of these grasses became highest in the Org6 rotation in Cycle 3, presumably because populations of those species best adapted to mowing built up in this rotation, especially in the relative absence of competition from tall broadleaf weeds that were less abundant in the Org6 rotation. It is of note that higher

Table 5. Correlation and standardized regression coefficients for factors significantly influencing weed presence and cover ($P < 0.01$).^a

Factor	Weed presence		Weed cover where present	
	Correlation	Logistic regression	Correlation	Least-squares regression
		<i>Amaranthus hybridus</i>		
Rotation length	-0.21	-0.62	-0.23	-0.25
Early-season temperature ^b	0.16	0.52	—	—
Tillage intensity	0.08	0.28	—	—
Crop competition	—	—	-0.16	-0.23
Other weed competition	—	—	-0.18	-0.23
Early-season precipitation ^b	—	—	0.19	0.19
R ²		0.247		0.172
		<i>Chenopodium album</i>		
Early-season temperature ^b	-0.51	-0.95	-0.48	-0.38
Rotation length	0.16	0.33	—	—
Crop competition	—	—	-0.23	-0.31
Midseason temperature ^b	—	—	-0.18	-0.26
Midseason precipitation ^b	—	—	-0.42	-0.14
R ²		0.424		0.362
		Annual grasses		
Early-season precipitation ^b	0.43	0.51	0.39	0.41
Early-season temperature ^b	0.33	0.30	—	—
Rotation length	0.13	0.19	—	—
Tillage intensity	0.09	-0.14	-0.10	-0.15
Crop competition	—	—	-0.10	-0.46
Midseason precipitation ^b	—	—	0.32	0.33
R ²		0.309		0.330

^aCorrelations are only shown for factors that made a significant contribution to regression models.

^bEarly-season temperature period for presence and cover variables was first 4 wk after planting. Early-season precipitation period for *A. hybridus* cover was 3 wk before to 1 wk after planting; for grass presence, first 5 wk after planting; and for grass cover, 2 wk before to 4 wk after planting. Midseason temperature period for *C. album* cover was 7 to 11 wk after planting. Midseason precipitation period for *C. album* cover was 5 to 8 wk after planting; and for grass cover, 9 to 13 wk after planting.

grass cover occurred most prominently in the corn phase of the Org6 rotation, which immediately followed the alfalfa crop (data not shown).

Factors Influencing Species Occurrence and Cover during Cycles 1 and 2

Amaranthus hybridus

The presence and cover of this species were weakly correlated to explanatory factors, and multiple regression models had relatively poor fit to data ($R^2 = 0.25$ and 0.17 for logistic and least-squares regressions, respectively). Because this species was present in greater than 90% of quadrants, the minimal correlation between factors and *A. hybridus* presence was not surprising. Length of crop rotation had the largest influence on *A. hybridus* presence and cover, based on relative magnitude of correlation and standardized regression coefficients (Table 5). This relationship was negative,

indicating that *A. hybridus* presence and cover declined as rotation length increased. This result is consistent with analyses presented in Tables 2–4, whereby the highest cover was in the shortest 2-yr rotation and the lowest cover was in the longest and most diverse rotation. In addition, factors of secondary importance included daily temperature during the early season (positive relationship to *A. hybridus* presence) and competition from crop and other weeds (negative relationships to *A. hybridus* cover).

The relative insensitivity of *A. hybridus* to all factors may be related, in part, to the coincidence of planting dates in this experiment with the optimum recruitment period for this species. Myers et al. (2004) demonstrated that *A. hybridus* emergence in milder mid-Atlantic sites occurred from early May to early July, with a mid-point of late May. Planting dates at FSP during Cycles 1 and 2 ranged from early May to late June, with a mean of May 27. Therefore, the pattern of planting dates at FSP coincided ideally with the emergence pattern of *A. hybridus* and would have provided highly favorable conditions for its emergence and growth. This would have enhanced its competitive capacity and minimized the effects of competition with crops or other weeds. *Amaranthus hybridus* is a C_4 plant that has higher rates of photosynthesis, water-use efficiency, and root-weight ratio than other weeds and crops (Patterson and Flint 1983; Seibert and Pearce 1993), and it would be expected to function best under warm, droughty conditions associated with later planting dates.

Although this species is capable of abundant seed production, Ullrich et al. (2011) demonstrated that seed viability at FSP was relatively short (half-life = 1.3 yr). This is undoubtedly the primary reason that longer rotations, which minimized recruitment and fecundity during years when corn and soybean were not grown, substantially reduced the seedbank and subsequent recruitment in years when row crops resumed (Teasdale et al. 2004). Thus, rotation of phenologically diverse crops was the major factor influencing this species (Table 5). However, the low overall model fit indicates that, despite rotational influences on seedbanks, there were other undefined factors and interactions that had a significant influence on the presence and abundance of this species.

Chenopodium album

Early-season temperature (average daily temperature during the first 4 wk after planting) was the dominating factor determining *C. album* presence and cover (Table 5). Correlation coefficients and standardized regression coefficients were highest for this factor, and overall model fit (R^2 values) was substantially higher for this species than for *A. hybridus*. Germination and emergence of *C. album* is known to be favored by cool temperatures, while warm temperatures can induce secondary dormancy (Bouwmeester and Karssen 1993). Therefore, it is not surprising that the probability of *C. album* presence had a strong negative association with early-season temperature (Figure 1A). This relationship was modified by rotation length, whereby longer rotations increased the probability of occurrence of this species, particularly at higher temperatures. For example, at an early-season average daily temperature of 23 C, the probability of *C. album* occurrence was 23%, 32%, and 64% in Org2, Org3, and Org6, respectively (Figure 1A). Germination of *C. album* is known to be stimulated by nitrate (Bouwmeester and Karssen 1993), and it is possible that mineralization of nitrogen from alfalfa residues that comprised the most significant portion of mineralizable nitrogen in Org6 (Spargo et al. 2011) resulted in greater emergence and occurrence of this species in this rotation. Warmer temperatures would be expected to enhance mineralization and nitrate release, increasing the probability of *C. album* presence in Org6, as observed in Figure 1A.

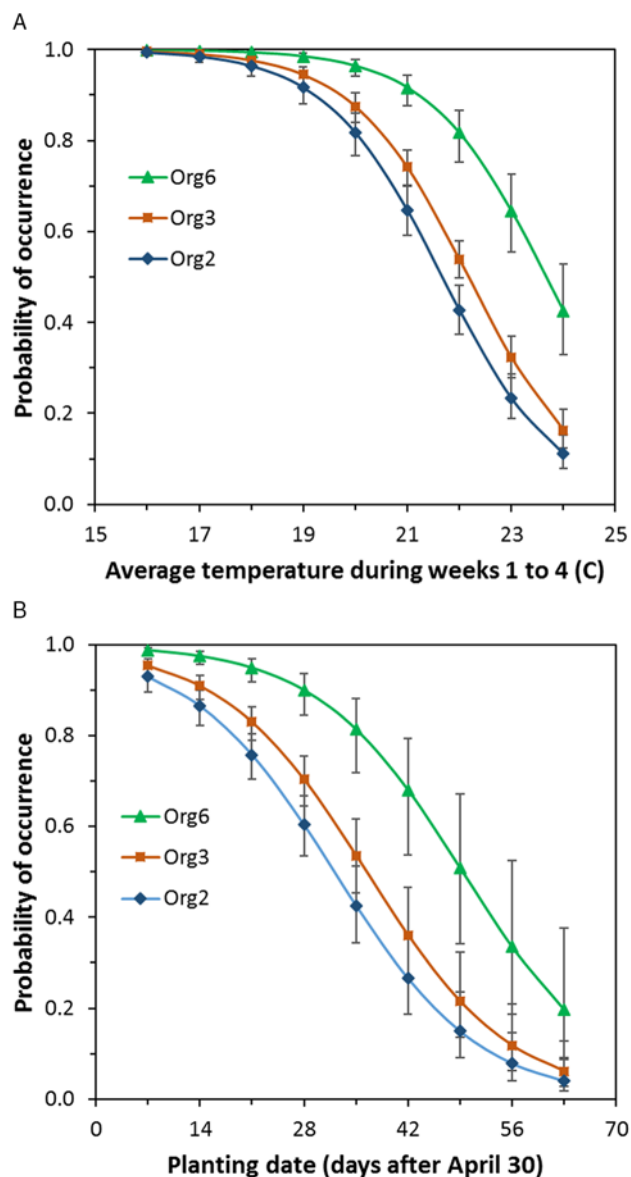


Figure 1. Predicted probability of occurrence of *Chenopodium album* as a function of (A) average daily temperature during the first 4 wk after planting and (B) planting date during Cycles 1 and 2 (1997–2008) at three organic rotational levels (Org2, 2-yr corn-soybean; Org3, 3-yr corn-soybean-wheat; and Org6, 6-yr corn-soybean-wheat-alfalfa). Probability estimated by logistic regression; bars represent the 95% confidence intervals.

Planting date was highly correlated with early-season temperature ($r = 0.84$), so the logistic regression of *C. album* occurrence with planting date in the absence of meteorological variables had a fit similar to that with the meteorological variables ($R^2 = 0.381$). The negative relationship with planting date was very similar to that with early temperature, and rotation modified the relation in a similar manner, increasing the probability of occurrence as rotation length increased (Figure 1B). Myers et al. (2004) demonstrated that *C. album* emergence began in early April and reached a midpoint in mid-May at milder mid-Atlantic sites. The response to planting date in Figure 1B fits this pattern, with high predicted *C. album* occurrence during the first 3 wk of May, and then falling substantially as planting dates were delayed into June. Other research also shows that *C. album* is more abundant at earlier

planting dates, whereas *A. hybridus* is more common at later dates (Wallace et al. 2018).

Annual Grasses

Increased precipitation early in the season resulted in a higher occurrence and cover of annual grasses (Table 5). For example, the logistic model predicted that a weekly precipitation total of 10 mm led to an annual grass occurrence of 31%, whereas weekly precipitation of 40 mm led to 85% occurrence. Many of the annual grass species encountered in this experiment are favored by mid- (Setaria species) to late-spring (*P. dichotomiflorum*, *E. crus-galli*, *D. sanguinalis*) emergence periods (Myers et al. 2004; Werle et al. 2014) as were encountered at FSP, and establishment of *P. dichotomiflorum* and *E. crus-galli* is favored by relatively wet soil conditions (Wiese and Vandiver 1970) as often occurred in spring. Generally, annual grasses remained persistent background species in this experiment, but rarely attained the cover levels of the dominant broadleaf species. Previous research at a nearby site showed that *S. faberi* was dominated by *A. hybridus* in tilled organic soils, particularly at June planting dates (Teasdale and Mirsky 2015).

The Progression of *Datura stramonium* and *Abutilon theophrasti* Cover

Datura stramonium

The homogeneity of slope test indicated a significant difference in *D. stramonium* logit cover progression among rotations ($P < 0.0001$). The slope of logit cover per unit progression year increased significantly in Org2 ($P < 0.0001$), but remained unchanged in Org3 ($P = 0.227$) and Org6 ($P = 0.082$). Although the homogeneity of slope analysis was conducted on a logit scale, regressions and means are shown graphically on the original cover scale for ease of conceptualization (Figure 2A). On the original cover scale, *D. stramonium* cover increased according to a quadratic function in Org2, reaching predicted levels between 20% and 30% in progression years 4 to 7. *Datura stramonium* mean cover did not exceed 11% in any year in Org3, and cover trends over seven yr after invasion did not change from initial levels recorded in the first year in Org3 or Org6.

The continuous row-crop environment in Org2 allowed for the rapid increase in *D. stramonium* cover to levels comparable with *A. hybridus*. The optimum period of *D. stramonium* emergence in mid- to late spring (Weaver and Warwick 1984; Werle et al. 2014) coincided with typical planting dates at FSP, and the long season of corn and soybean allowed it to produce viable seed before harvest. *Datura stramonium* has an order of magnitude larger seed mass than *A. hybridus* and *C. album*, as well as a larger seed mass than the grasses in this experiment (Weaver and Warwick 1984). This would permit emergence from deeper in the soil profile than these other species and would allow it to root below and better survive rotary hoeing operations that only disturb the surface soil. Tolerance of wet soil, a condition not uncommon at FSP in spring, and its responsiveness to organic amendments such as manure and compost (Weaver and Warwick 1984) are traits that would allow *D. stramonium* to thrive in these organic rotations. Therefore, under the continuous spring planting regime of Org2 crops, this weed had optimum conditions to multiply annually and become a codominant species within a few years of invasion. Remarkably, the presence of a rotational wheat crop for only 1 out of every 3 yr in Org3 was sufficient to break this cycle and prevent an escalation of *D. stramonium* cover. Given that it took

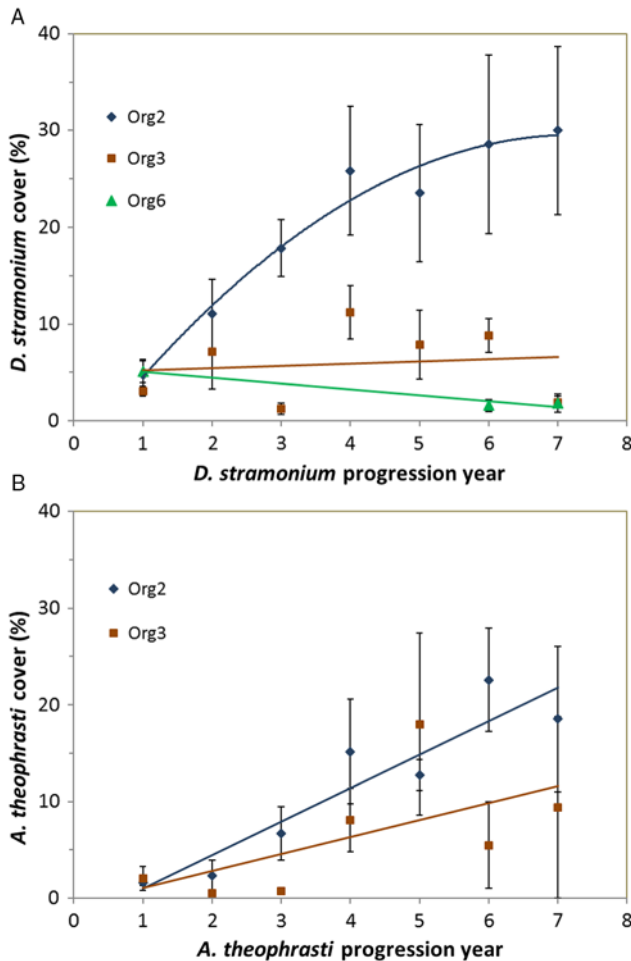


Figure 2. *Datura stramonium* (A) and *Abutilon theophrasti* (B) cover as a function of progression year following the initial occurrence of these species into a quadrant at year = 1 in the 2-yr (Org2), 3-yr (Org3), and 6-yr (Org6) rotations. Points represent means with SE bars. Lines are least-squares regression estimates. There were insufficient *A. theophrasti* Org6 data for analysis of this rotation.

4 yr to build sufficient populations to achieve high weed cover levels in Org2 (Figure 2A), the presence of a wheat crop every third year in Org3 apparently reset populations to initial levels and never allowed larger populations to establish. Similarly, the longer Org6 rotation, in which spring-planted row crops only occurred 2 out of 6 yr, also suppressed potential population growth of this species (Figure 2A). In addition, the midsummer harvesting operations associated with the winter annual wheat and perennial alfalfa crops became important filters that restricted invasion of this species in the Org3 and Org6 rotations.

Abutilon theophrasti

The homogeneity of slope test showed that *A. theophrasti* logit cover increased significantly more in Org2 than in Org3 ($P = 0.004$). The slope of *A. theophrasti* logit cover increased significantly in both Org2 ($P < 0.0001$) and Org3 ($P = 0.015$). On an untransformed cover scale, *A. theophrasti* cover reached levels of approximately 20% and 10% after 7 yr in Org2 and Org3, respectively (Figure 2B). *Abutilon theophrasti* is similar to *D. stramonium* in several traits, including phenology of emergence and seed production, seed mass, seed longevity in soil, plant stature, physiology, and response to fertility (Patterson and Flint 1983; Warwick and

Black 1988), accounting for its capacity to more successfully invade and multiply in Org2 than in Org3 quadrants. Although there were insufficient Org6 data for this rotation to be analyzed, *A. theophrasti* is usually associated with tilled-soil environments (Bernstein et al. 2014), so it would likely be suppressed by a 3-yr period without tillage during the alfalfa phase of the Org6 rotation.

Traits Selected by Organic Grain Crop Rotations

Common Traits

There were relatively few dominant weed species in organic grain crops at the FSP site during the first 18 yr of this experiment. *Amaranthus hybridus*, *C. album*, *E. canadensis*, *D. stramonium*, and *A. theophrasti* were the most prominent species exhibiting high soil cover in selected years and quadrants. These species share many traits adapted to organic farming operations. They all are tall, erect annual broadleaf weeds that can grow into gaps in the corn or above the soybean leaf canopy. With the exception of *E. canadensis* (whose unique niche was discussed earlier), their emergence period is either in late spring and/or can occur over an extended duration in spring and early summer, giving them adaptability to the varying tillage and planting dates that occurred at FSP. They possess several dormancy-breaking mechanisms (including cold-moist afterripening, light, nitrates, alternating temperatures, and seed coat scarification) that would typically be observed in soils that receive tillage during seedbed preparation in spring. They are highly responsive to nutrients released from organic amendments and produce seeds in late summer, making them well adapted to the nutrient environment and long growing season required by corn and soybean. Finally, with the exception of *E. canadensis*, they produce large numbers of dormant seeds, a portion of which are capable of several years' duration in the soil seedbank, ensuring population survival during years with unfavorable establishment and growing conditions and significantly contributing to the storage effect, a mechanism to be discussed in the next section. These highly correlated traits are typical of early-succession annual species inhabiting disturbed sites (Rees et al. 2001).

Role of the Storage Effect

The dominant species in FSP organic cropping environments persisted because of divergent traits that allowed them to respond differently to environmental fluctuations and management practices, according to a process called "the storage effect." Storage effect theory defines three conditions necessary for species persistence in the weed community: first, there must be species-specific responses to fluctuating environmental conditions; second, the differential species responses to the environment should lead to differential competition (covariance between environment and competition); and third, a life-history trait, such as seedbank persistence, must buffer population growth against unfavorable years (Angert et al. 2009; Facelli et al. 2005; Miller et al. 2012; Rees et al. 2001). All of these conditions were met in the rotational systems reported for FSP organic rotations. First, as germination requirements are often more restrictive than vegetative growth requirements (Facelli et al. 2005), variation in the timing and extent of emergence in response to annual operational and environmental conditions played an important role in defining species-specific responses. Second, as the timing and abundance of emergence is an important determinant of competition, environmental and competition effects would be expected to covary and lead to differential competitive outcomes among species in different years.

Finally, given the multiyear persistence of the seedbank of these species, all would have the capacity for buffered populations during low-density conditions.

Organic cropping systems, including those in this experiment, are characterized by annual soil disturbance. Disturbance can be an important factor in generating the storage effect when it creates differential environmental conditions that would differentially enhance germination of weed species in the seedbank (Chesson and Huntly 1997; Dinnage 2009), and this has been shown to be particularly true in the case of spring tillage (Miller et al. 2012). Spring tillage stimulates germination of summer weeds differently depending on annual environmental cues, leading to annual variation in emergence and, consequently, to covariance between environment and competition, which is a necessary condition for the storage effect. Annual spring tillage in preparation for planting summer grain crops at FSP occurred over a range of almost 2 mo, which generated a wide range of annual environmental conditions with consequent effects on species performance, as we showed earlier. Early-season temperature was highly correlated with planting date, and both were shown to have significant effects on the differential presence and cover of species in this experiment. Earlier plantings without tillage favored species such as *C. album*, *E. canadensis*, and *Persicaria* sp., which favor cooler early-spring conditions, whereas late plantings following tillage favored *A. hybridus*, *D. stramonium*, *A. theophrasti*, *Ipomoea* sp., and grasses that favored warmer late-spring conditions (also confirmed by research at other locations; Bernstein et al. 2014; Wallace et al. 2018). Thus, the fluctuating timing of primary tillage was a significant filter for differentiating species presence and cover in a given year and provided the variable annual conditions defining the behavior of this weed community according to the storage effect.

Management Implications

This long-term research supports the management principle that diverse rotations can further diversify the filtering of species traits and reduce dominance by species with traits most adapted to summer annual crops. Organic crop rotations that introduced winter annual crops planted in fall and perennial forage crops created important filters that prevented establishment and seed production by the dominant summer annual species favored by the summer annual grain crops in this experiment. As shown earlier, by regularly imposing conditions that altered the soil-disturbance patterns and harvesting sequences associated with summer annual crops, these phenologically diverse rotations limited the population growth of summer annual weeds. Reliance on soil disturbance for organic production, whether primary tillage for seedbed preparation or rotary hoeing and sweep cultivation for postplant weed removal, can also have negative effects on the environment, including enhanced greenhouse gas emissions, nitrate and soil losses, and reduced carbon sequestration (Cavigelli et al. 2013; Trewavas 2004; Tuomisto et al. 2012). More diverse rotations including winter annual grain crops and perennial hay crops can mitigate against soil losses and greenhouse gas emissions (Cavigelli et al. 2013), as well as disrupt life cycles of dominant weed species.

Although the FSP experiment included only agronomic crops, rotations including short-season vegetable crops have been shown to impose even more restrictive filters by imposing tillage at various intervals throughout the growing season. This interrupts the life cycle of summer annual species requiring a full season for reproduction in favor of generalist species with more flexible emergence and early reproductive traits (Mohler et al. 2018). There is currently a need for greater vegetable and lower commodity crop

production to meet world dietary requirements (KC et al. 2018) and the proximity of population centers to agricultural production fields in the mid-Atlantic area would facilitate delivery of more nutritionally balanced products. Accordingly, the development of diverse crop rotations including grain, forage, and vegetable crops would provision a more balanced food diet and could provide flexibility in imposing more diverse disturbance patterns into crop rotations, thereby leading to a more balanced and manageable community of weed species. Creative approaches to alternating crops as well as tillage patterns (Anderson 2010) could interrupt weed life cycles, provide for stewardship of soil resources, and produce a more nutritious diet for future generations.

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