Crop rotation and tillage system effects on weed seedbanks

Authors: John Cardina, Catherine P. Herms, and Douglas J. Doohan

Crop rotation and tillage system effects on weed seedbanks

John Cardina
Corresponding author. Department of Horticulture and Crop Science, Ohio Agricultural Research and Development Center, Wooster, OH 44691; cardina.2@osu.edu

Catherine P. Herms
Douglas J. Doohan
Department of Horticulture and Crop Science, Ohio Agricultural Research and Development Center, Wooster, OH 44691

We characterized the size and species composition of the weed seedbank after 35 yr of continuous crop rotation and tillage system treatments at two locations in Ohio. Spring seedbanks were monitored during 1997, 1998, and 1999 in continuous corn (CCC), corn–soybean (CS), and corn–oats–hay (COH) rotations in moldboard plow (MP), chisel plow (CP), and no-tillage (NT) plots where the same herbicide was used for a given crop each growing season. There were 47 species at Wooster and 45 species at Hoytville, with 37 species occurring at both locations in all 3 yr. Crop rotation was a more important determinant of seed density than was tillage system. Seed density was highest in NT and generally declined as tillage intensity increased. Seeds accumulated near the surface (0 to 5 cm) in NT but were uniformly distributed with depth in other tillage systems. At both locations there was a significant interaction between tillage and rotation for estimates of the total seed density. Seed density was highest in NT-CCC, with 26,850 seeds m^{-2} at Wooster and 8,680 seeds m^{-2} at Hoytville. At Wooster total seed density in CCC plots was 45 and 60% lower than in COH plots for CP and MP. In NT the total seed density was 40% greater in CCC than in COH. At Hoytville total seed density in CCC plots was 72% lower than in COH plots that were CP or MP, whereas seed density was 45% higher in CCC than in COH plots that were in an NT system. There were more significant differences in seedbank density for any given species for crop rotation than for tillage treatments. Seed densities of three broadleaves (shepherd's-purse, Pennsylvania smartweed, and corn speedwell) at Wooster and four broadleaves (yellow woodsorrel, redroot pigweed, Pennsylvania smartweed, and spotted spurge) at Hoytville were more abundant in COH (140 to 630 seeds m^{-2}) than in CS (10 to 270 seeds m^{-2}) or CCC (< 1 to 60 seeds m^{-2}), regardless of the tillage system. At both locations Pennsylvania smartweed seeds were more abundant in COH (260 and 630 seeds m^{-2}) than in other rotations (10 to 20 seeds m^{-2}). Relative importance (RI) values, based on relative density and relative frequency of each species, were lower in CS than in CCC for common lambsquarters and five other weeds at Wooster; RI of giant foxtail was 80% lower in COH than in CCC at Hoytville. The data show how species composition and abundance change in response to crop and soil management. The results can help to determine how complex plant communities are "assembled" from a pool of species by specific constraints or filters.

Crop rotation and tillage system are among the many agronomic variables that interact with weed management to affect the size and composition of the weed seedbank. Agronomic variables alter the effectiveness of weed management tactics by favoring some plant traits and filtering out others (Drake et al. 1999). This type of selection can operate at the seed, seedling, or reproductive stages to result in additions to or losses of species in the plant community. In this way, changes in the weed seedbank are an important indicator of how past and current soil, crop, and weed management efforts interact with environmental conditions over time to assemble a particular weed community (Drake et al. 1999).

Crop rotations affect seedbanks because weed control measures change with successive crops (Ball 1992; Ball and Miller 1990). Weeds that survive and produce seeds in one crop contribute to the seedbank from which weed seedlings are recruited in successive crops. Because of greater variability in the type and timing of soil, crop, and weed management practices, there are more opportunities for weed mortality events in rotations than in monoculture (Martin and Felton 1993). However, this variability may also provide more chances for successful weed emergence, establishment, and seed production in rotations than in monoculture (Dorado et al. 1999). The balance of these should be reflected in the weed seedbank. Where crops are rotated, weed communities are more diverse than where crops are grown in monoculture (Dorado et al. 1999; Liebman and Dyck 1993). In the few studies where rotation effects on weeds have been examined without herbicides as a confounding factor, rotation by itself led to reduced weed populations, especially where a small grain was included in the rotation

(Liebman and Dyck 1993; Schreiber 1992). This effect of small grains was attributed to allelopathy and to increased exposure to predators and pathogens, especially for summer annual weed seeds that remain in the soil during the wheat phase of the rotation (Liebman and Dyck 1993; Schreiber 1992). However, there have been few long-term studies where the effects of crop rotation on weed seedbanks have been examined.

Tillage systems have been shown to affect the depth distribution, abundance, and species composition of seeds in the soil. Weed seeds accumulate near the soil surface in no-till (NT) and are more or less uniformly distributed with depth by moldboard plowing (MP) in combination with disking (Ball 1992; Yenish et al. 1992). These differences in seed burial depth affect weed community composition because species whose seeds survive, germinate, and emerge at or near the soil surface tend to increase in reduced tillage systems (Buhler 1995). Species that depend on seed burial to break dormancy, to protect them from surface seed predators, or to ensure successful establishment are better adapted to MP and other tillage systems (Buhler 1995). Several studies have indicated that perennial weeds increase after several years of reduced tillage because of increased seed accumulation at the soil surface and reduced disturbance of vegetative propagules compared with plowed systems (Barberi et al. 1998; Cardina et al. 1991; Triplett and Lytle 1972; Wicks et al. 1994). In contrast, Derksen et al. (1994) found an increase in wind-dispersed species and volunteer crops, but not perennial weeds, in reduced tillage fields in Saskatchewan.

Soil properties and other site characteristics that influence biological activity and seed dormancy have been associated with variations in the species composition of seedbanks (Kremer 1993; Thompson and Grime 1979). Forcella et al. (1992) reported large differences in seed density and species composition in seedbank samples collected from eight midwestern states, where soil types ranged from sandy loams to clay loams. Previously, we reported that the effect of three tillage systems on seed depth distribution differed with soil type, especially for NT, where seeds were retained at the surface in a crusting soil but were distributed deeper in soil with a high shrink–swell capacity (Cardina et al. 1991).

Effects of crop rotations and tillage systems on soil characteristics, crop productivity, and weed communities require several years to stabilize (Dick and Daniel 1987). Crop rotation and tillage studies established in 1963 on two soil types in Ohio are a good source for determining how long-term crop and soil management affect the abundance and composition of weed seeds in soil. After about 20 yr, soil chemical and biological characteristics at various soil depths varied with tillage system and sometimes interacted with crop rotation (Dick et al. 1986). Although no weed data were collected at the beginning of these studies, every crop appears every year, and the same herbicides were generally used in all tillage systems for a given crop. The objective of this study was to evaluate the long-term influence of tillage systems, crop rotation, and their interaction on the weed community represented in the soil seedbank.

Materials and Methods

Experiments were initiated in 1963 at Wooster, OH, on a moderately well-drained Wooster silt loam forest soil (Typ-

ic fragiudalf with 25% sand, 60% silt, 15% clay, and 2.4% organic matter) and at Hoytville, OH, on a poorly drained silty clay loam lake-bed soil (Mollic ochraqualf with 21% sand, 42% silt, 37% clay, and 5.7% organic matter). Other soil and site characteristics for these studies, as well as details of experimental design, were described by Dick and Van Doren (1985). The Wooster site was established in an old grass meadow, whereas the Hoytville site was in a corn–oats–meadow rotation 5 yr before the experiment.

The experimental design at each site is a randomized complete block with three replications. Crop rotation treatments, with every crop appearing each year, are continuous corn (CCC); corn–soybean and soybean–corn (CS); and corn–oats–hay, oats–hay–corn, and hay–corn–oats (COH). These three rotation sequences were applied in a factorial combination with three tillage treatments. MP was done to a depth of 20 to 25 cm, followed by two 10-cm-deep secondary tillage operations before planting. The chisel plow (CP) treatment was imposed from 1985, but the plot had previously been tilled with a paraplow (1983–1984) or shallow MP without subsequent disking (1963–1982). NT plots received only the in-row tillage caused by a coulter planter. Tillage operations were performed in spring at Wooster and in the fall at Hoytville. Before 1985 the MP and CP plots were occasionally cultivated for weed management at the Wooster site only.

Plots at Wooster are 5 m wide and 21 m long; those at Hoytville are 6 m wide and 30 m long. Corn was planted in rows 102 cm apart from 1967 to 1972 and 76 cm apart since 1973. Soybeans were planted at these same row widths, but since 1985 they have been drilled in rows 18 cm apart. Oats and alfalfa (*Medicago sativa* L.) hay crops were initially planted with conventional grain drills, but since 1980 no-till drills have been used. Each year, corn populations were thinned to a common density. Some management variables other than tillage and crop rotation (e.g., crop varieties, fertilizer rates, crop densities, row widths, and herbicides) have been modified over time to conform to accepted agronomic practices. Fertilizer has been applied according to Ohio State University soil test recommendations, with the same rates of N, P, and K applied to each tillage system. Lime has been broadcast as required to maintain a pH of about 6.0 in the Ap horizon. Information on cultivars, fertilizer rates, insecticide rates, and herbicides has been documented (Dick and Van Doren 1985; Dick et al. 1986).

Within a crop and year at a given location, the same herbicides and rates have been used in all tillage systems, except that glyphosate was applied to NT plots for preplant weed control beginning in 1974, and paraquat was substituted for glyphosate from 1985 to 1989. The names and rates of the herbicides used since 1994 are given in Table 1. In the years before 1997, atrazine, simazine, or cyanazine was applied to corn at rates from 1.1 to 4.5 kg ha^{-1}. Amitrole was applied from 1963 to 1967, and dicamba plus linuron or alachlor was applied at labeled rates from 1967 to 1984. In soybean, metribuzin plus linuron, alachlor, or metolachlor was applied during the first 10 yr of the study. Within the last 8 yr, acetolactate synthase inhibitors have been the primary soybean herbicides, with other products applied as needed. Dicamba was occasionally used in oats to reduce infestations of broadleaf weeds. No herbicides were used in hay crops, except for glyphosate before seeding

TABLE 1. Herbicides[a] applied to corn and soybean crops at Wooster and Hoytville from 1994 through 1998. At Wooster, no-till (NT) oats and hay crops received applications of glyphosate (2.2 kg ai/ha) before planting each year, except in 1996 when 2,4-D plus dicamba (0.42 + 0.14 kg ai/ha) was applied before planting. At Hoytville NT oats and hay crops received glyphosate (2.2 kg ai/ha) before planting; all oats plots received 2,4-D (0.42 kg ai/ha) plus dicamba (0.14 kg ai/ha) for broadleaf weed control.

| | Wooster | | | | Hoytville | | | |
| | Corn | | Soybean | | Corn | | Soybean | |
Year	Herbicide	Rate	Herbicide	Rate	Herbicide	Rate	Herbicide	Rate
		kg ai/ha		kg ai/ha		kg ai/ha		kg ai/ha
1994	Glyphosate[b]	2.2	Glyphosate	2.2	Glyphosate	2.2	Glyphosate	2.2
	Linuron	0.85	Linuron	0.84	Atrazine	1.12	Metolachlor	1.12
	Alachlor	2.2	Chlorimuron	0.03	Cyanazine	3.4	Metribuzin	0.21
	Cyanazine	2.2	Metolachlor	2.2	2,4-D	0.56	Chlorimuron	0.21
	Clopyralid	0.18			Alachlor	1.12		
					Bentazon	1.12		
1995	Glyphosate	2.2	Glyphosate	2.2	Glyphosate	1.68	Glyphosate	1.68
	Pendimethalin	1.4	Metribuzin	0.56	2,4-D	0.56	Chlorimuron	0.004
	Atrazine	1.0	Acetochlor	1.0	Atrazine	2.2	Thifensulfuron	0.002
	Dicamba	0.56			Cyanazine	1.0	Clethodim	0.175
	Simazine	1.1			2,4-D	0.56		
	Cyanazine	1.7						
1996	Metolachlor	2.4	Alachlor	0.84	Glyphosate	1.12	Glyphosate	2.2
	Flumetsulam	0.063	Linuron	0.84	Atrazine	1.2	Chlorimuron	0.008
	Atrazine	1.8	Chlorimuron	0.03	Bentazon	1.2	Thifensulfuron	0.004
	2,4-D	0.56					Clethodim	0.175
	Cyanazine	1.1						
1997	Glyphosate	1.12	Metribuzin	0.56	Glyphosate	0.56	Glyphosate	2.2
	Pendimethalin	1.4	Metolachlor	2.18	Acetochlor	1.8	Imazethapyr	0.07
	Atrazine	1.8			Atrazine	1.5	Bentazon	0.56
	Cyanazine	1.1			2,4-D	0.56	Acifluorfen	1.12
					Clopyralid	0.29	Clethodium	0.14
					Bentazon	1.12		
1998	Glyphosate	1.7	Glyphosate	1.68	Glyphosate	0.56	Glyphosate	2.2
	Metolachlor	2.4	Metolachlor	2.4	Acetochlor	2.1	Dimethenamid	1.68
	Flumetsulam	0.063	Flumetsulam	0.063	Atrazine	1.12	Glyphosate	1.12
	Atrazine	1.1			2,4-D	0.56		
	2,4-D	0.56			Nicosulfuron	0.03		

[a] Glyphosate = N-phosphonomethyl glycine; linuron = N'-(3,4-dichlorophenyl)-N-methoxy-N-methylurea; alachlor = 2-chloro-N-(2,6-diethylphenyl)-N-(methoxymethyl)acetamide; cyanazine = 2-[[4-chloro-6-(ethylamino)-1,3,5-triazin-2-yl]amino]-2-methylpropanenitrile; clopyralid = 3,6-dichloro-2-pyridinecarboxylic acid; pendimethalin = N-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine; dicamba = 3,6-dichloro-2-methoxybenzoic acid; simazine = 6-chloro-N,N'-diethyl-1,3,5-triazine-2,4-diamine; metolachlor = 2-chloro-N-(2-ethyl-6-methylphenyl)-N-(2-methoxyl-1-methylethyl)acetamide; flumetsulam = N-(2,6-difluorophenyl)-5-methyl[1,2,4]triazolo[1,5-a]pyrimidine-2-sulfonamide; 2,4-D = (2,4-dichlorophenoxy)acetic acid; chlorimuron = 2-[[[[(4-chloro-6-methoxy-2-pyrimidinyl)amino]carbonyl]amino]sulfonyl]]benzoic acid; metribuzin = 4-amino-6-(1,1-dimethylethyl)-3-(methylthio)-1,2,4-triazin-5(4H)-one; acetochlor = 2-chloro-N-(ethoxymethyl)-N-(2-ethyl-6-ethylphenyl)acetamide; nicosulfuron = 2-[[[[[(4,6-dimethoxy-2-pyrimidinyl)amino]carbonyl]amino]sulfonyl]-N,N-dimethyl-3-pyridinecarboxamide; thifensulfuron = 3-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]amino]sulfonyl]-2-thiophenecarboxylic acid; clethodium = (E,E)-($\pm$)-2-[1-[[[(3-chloro-2-propenyl)oxy]imino]propyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one; imazethapyr = 2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-ethyl-3-pyridinecarboxylic acid; acifluorfen = 5-[2-chloro-4-(trifluoromethyl)phenoxy]-2-nitrobenzoic acid; dimethenamid = 2-chloro-N-[(1-methyl-2-methoxy)ethyl]-N-(2,4-dimethyl-thien-3-yl)-acetamide.

[b] Glyphosate was applied to NT plots only.

in NT plots. All decisions on herbicide selection and rates were made by the farm manager, who strived to maintain excellent weed control in all crops.

Seedbanks were sampled during the third week of March 1997, 1998, and 1999. Eighteen soil cores, 3.5 cm in diameter and 10 cm deep, were obtained at random from each plot. An additional set of 18 soil cores obtained from the CCC plots were divided into 0- to 5-, 5- to 10-, 10- to 15-, and 15- to 20-cm depths. Cores of a given depth were pooled for each plot. Soil was processed as soon as possible by sieving through a 0.64-cm screen to break up large soil clods. The seedbank was characterized using the greenhouse germination methods described previously (Cardina and Sparrow 1996). Briefly, an entire sample, minus large stones and root fragments, was spread in a 22-cm² tray, which was placed on a sand bed and subirrigated. The greenhouse was set to day and night temperatures of 18 and 8 C, respectively, to simulate spring field conditions, with no artificial lighting. Emerged weed seedlings were identified, counted, and removed. After emergence ceased, samples were stirred, resieved, and placed in a 4 C cold room for 3 wk followed by 1 wk at alternating temperatures (15 and 4 C) before being returned to the greenhouse. This process was repeated twice, after which time no additional seedlings emerged.

Data were subjected to analysis of variance after log transformation, and back transformed to numbers of germinated seeds per square meter for tabulation and graphing. Seed density data for individual species, whose log-transformed data met assumptions of analysis of variance (ANOVA), and total seed numbers for all species were compared across the

three rotations and three tillage systems, using a four-factor (rotation, tillage, replication, year) repeated measures model in the GLM and MIXED procedures of SAS.[1] The Huynh–Feldt method was used to adjust degrees of freedom of the within-subject ANOVA tests (Huynh and Feldt 1970). Where there was no tillage-by-rotation interaction, these main factors are discussed separately. Where interactions occurred, data were plotted to determine the factors responsible and the biological significance. Where appropriate, single–degree of freedom contrasts were used to compare main effect means in the presence of interactions. Because our objective was to examine the overall long-term effects of crop rotation, the rotation treatments were analyzed as three composite rotations. Thus, data for corn–soybean–corn and soybean–corn–soybean were combined (designated CS), as were data for corn–oats–hay, oats–hay–corn, and hay–corn–oats (designated COH). The repeated measures ANOVA indicated no significant interactions of year with tillage or rotation; therefore, data for the three sampling years were combined. Depth was included in the ANOVA model as a fixed effect for the CCC data where samples were obtained from four depths.

A relative importance (RI) index was calculated from the density data for each species as a measure of both relative density (rD = density of weed x/total weed density) and relative frequency (rF = absolute frequency of weed x/total absolute frequency of all weeds, where absolute frequency = the number of samples with weed x/total number of samples). The RI was calculated as (rD + rF)/2. Average RI values for each plot were ranked by the order of magnitude in the NT treatments for comparisons of tillage systems and in the order of CCC treatments for comparisons of crop rotations. Differences in RI rankings among species were determined from the Kruskal–Wallis statistic (Steel and Torrie 1980).

Results and Discussion

Species Composition

Springtime seedbanks included 47 species at Wooster and 45 species at Hoytville, with 37 species occurring at both locations in all 3 yr (Table 2). Thirteen species accounted for most of the variability among tillage and rotation plots at both locations. Tillage affected seed density of redroot pigweed, common lambsquarters, yellow woodsorrel, fall panicum (*Panicum dichotomiflorum* Michx.), giant foxtail, common chickweed [*Stellaria media* (L.) Vill.], and corn speedwell at Wooster, and common lambsquarters, barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.], spotted spurge, yellow woodsorrel, and giant foxtail at Hoytville. Crop rotation affected seed density of shepherd's-purse, common lambsquarters, yellow woodsorrel, witchgrass (*Panicum capillare* L.), broadleaf plantain (*Plantago major* L.), Pennsylvania smartweed, giant foxtail, yellow foxtail [*Setaria pumila* (Poir.) Roem & Schult], common chickweed, and corn speedwell at Wooster, and redroot pigweed, large crabgrass (*Digitaria sanguinalis* L.), barnyardgrass, yellow woodsorrel, fall panicum, Pennsylvania smartweed, giant foxtail, and yellow foxtail at Hoytville. The interaction of tillage system with crop rotation was significant for seed density of common lambsquarters, yellow woodsorrel, fall panicum, and giant foxtail at Wooster, and redroot pigweed, large crab-

grass, barnyardgrass, yellow woodsorrel, fall panicum, Pennsylvania smartweed, giant foxtail, and yellow foxtail at Hoytville. Thirty-three species at Wooster and 34 at Hoytville appeared in only 1 or 2 yr and had total densities of less than 20 individuals, and there were fewer than 10 individuals in any year. The seedbank data for these weeds did not meet the assumptions of ANOVA, even after transformation, and were therefore not subjected to ANOVA. There were more significant differences in seedbank density for any given species for crop rotation than for tillage treatments.

Main Effects of Tillage

Seed Depth

The effect of tillage system on seed depth was studied for CCC plots only. There are no indications in previous reports that crop rotation affects seed depth apart from the tillage equipment used to manage the crops in the rotation. Seed density was not affected by year or by interactions of year with tillage or depth at either location (data not shown). Repeated measures ANOVA showed no effect of year or interactions of year with tillage or depth on seed density at either location (data not shown). There were significant effects of tillage and depth, and a tillage-by-depth interaction for total seed density at both locations (Figures 1a and 1c). The number of seeds was highest in NT at all depths and generally declined as tillage intensity increased. In NT the density of seeds near the surface (0 to 5 cm) was about four times as high as the density 5 to 10 cm deep and over six times as high as the density 15 to 20 cm deep at both locations. Seed density did not differ with depth in the MP plots at either location ($\bar{x}$ = 440 seeds m^{-2} at Wooster and 190 seeds m^{-2} at Hoytville), and the only difference in the CP plots was between 0- to 5-cm (1,100 seeds m^{-2}) and 15- to 20-cm (570 seeds m^{-2}) depths at Wooster. These findings are consistent with previous reports on the effect of tillage on seed burial depth (Ball 1992; Yenish et al. 1992). Shifts in weed species in different tillage systems have been attributed to seed burial and to differences in emergence patterns of seeds buried at different depths (Buhler 1995).

There was a significant effect of depth and a depth-by-tillage interaction for a number of species in the seedbank at Wooster (Figure 1b) but not at Hoytville (Figure 1d). At Wooster 6.7 species were found 0 to 5 cm deep in NT, 4.2 in CP, and 3.4 in MP plots (Figure 1b). In NT plots a higher number of species (6.7) was found in the surface 5 cm than at 10- to 15- and 15- to 20-cm depth (3.9). This pattern reflects the continual deposition of seeds at the surface and the probable decay of seeds of some species with depth. In MP the number of species in the seedbank did not differ with depth ($\bar{x}$ = 2.4 to 3.4). In CP plots, germinable seeds of 4.2 species were present at 0- to 5-cm depth and of 2.4 species at 15- to 20-cm depth, and there was no difference at the intermediate depths (3.4 to 3.7 species). Common lambsquarters was the most abundant species at all depths, accounting for 48 to 81% of the total seed density, with no consistent pattern in species composition among depths across tillage systems (data not shown). At Hoytville, where the average number of species per plot was 30 to 50% lower than at Wooster, there were no depth or tillage-by-depth effects for species number per plot. The lack of a depth effect for this location is consistent with

TABLE 2. Overall effects of tillage (T) and rotation (R) on weed seed density of species occurring in Wooster and Hoytville, OH, from 1997 to 1999.[a]

			Wooster			Hoytville		
Latin name	Common name	Bayer code	T	R	T × R	T	R	T × R
Abutilon theophrasti Medicus	Velvetleaf	ABUTH	.	.	.	.	.	.
Acalypha virginica L.	Virginia copperleaf	ACCVI	0.0321	NS	NS	.	.	.
Amaranthus retroflexus L.	Redroot pigweed	AMARE	.	.	.	NS	0.0001	NS
Ambrosia artemisiifolia L.	Common ragweed	AMBEL	—	—	—	.	.	.
Anagallis arvensis L.	Scarlet pimpernel	ANGAR	.	.	.	.	.	.
Apocynum cannabinum L.	Hemp dogbane	APCCA	—	—	—	.	.	.
Atriplex patula L.	Spreading orach	ATXPA	—	—	—	.	.	.
Brassica kaber (DC.) L.C. Wheeler	Wild mustard	SINAR	NS	.	.	.	.	.
Capsella bursa-pastoris (L.) Medicus	Shepherd's-purse	CAPBP	NS	0.0001	NS	.	.	.
Cardamine hirsuta L.	Hairy bittercress	CARHI	.	.	.	.	.	.
Chenopodium album L.	Common lambsquarters	CHEAL	0.0032	0.0001	0.0001	0.0017	NS	NS
Cirsium arvense (L.) Scop.	Canada thistle	CIRAR	.	.	.	.	.	.
Cirsium vulgare (Savi) Tenore	Bull thistle	CIRVU	—	—	—	.	.	.
Conyza canadensis (L.) Cronq.	Horseweed	ERICA	.	.	.	.	.	.
Cyperus esculentus L.	Yellow nutsedge	CYPES	.	.	.	.	.	.
Daucus carota L.	Wild carrot	DAUCA	—	—	—	.	.	.
Digitaria sanguinalis (L.) Scop.	Large crabgrass	DIGSA	NS	0.0001	NS	NS	0.0004	NS
Echinochloa crus-galli (L.) Beauv.	Barnyardgrass	ECHCG	.	.	.	0.0113	0.0060	NS
Elytrigia repens (L.) Nevski	Quackgrass	AGRRE	—	—	—	.	.	—
Erechtites hieracifolia (L.) Raf. ex DC.	American burnweed	EREHI	.	.	.	.	.	.
Erigeron annuus (L.) Pers.	Annual fleabane	ERIAN	.	.	.	NS	NS	NS
Euphorbia maculata L.	Spotted spurge	EPHMA	—	—	—	0.0017	NS	—
Festuca arundinacea Schreb.	Tall fescue	FESAR	.	.	.	—	—	—
Glechoma hederacea L.	Ground ivy	GLEHE	.	.	.	—	—	—
Juncus tenuis Willd.	Slender rush	IUNTE	.	.	.	—	—	—
Lactuca serriola L.	Prickly lettuce	LACSE	.	.	.	—	—	—
Lamium amplexicaule L.	Henbit	LAMAM	.	.	.	—	—	—
Lamium purpureum L.	Purple deadnettle	LAMPU	.	.	.	—	—	—
Lobelia inflata L.	Indiantobacco	LOBIN	.	.	.	—	—	—
Malva neglecta Wallar.	Common mallow	MALNE	.	.	.	.	.	.
Melilotus alba Medicus	White sweetclover	MEUAL	.	.	.	.	.	.
Muhlenbergia schreberi J.F. Gmel.	Nimblewill	MUHSC	.	.	.	—	—	—
Oxalis stricta L.	Yellow woodsorrel	OXAST	0.0001	0.0001	0.0027	0.0059	0.0287	NS
Panicum capillare L.	Witchgrass	PANCA	NS	0.0001	NS	.	.	.
Panicum dichotomiflorum Michx.	Fall panicum	PANDI	0.0001	NS	0.0023	NS	0.0001	NS
Physalis subglabrata Mackenz. & Bush	Smooth groundcherry	PHYSU	NS	—	NS	.	.	.
Plantago major L.	Broadleaf plantain	PLAMA	NS	0.0001	—	.	.	.
Poa annua L.	Annual bluegrass	POAAN	.	.	.	.	.	.
Polygonum aviculare L.	Prostrate knotweed	POLAV	.	.	.	—	—	—
Polygonum convolvulus L.	Wild buckwheat	POLCO	—	—	—	.	.	.
Polygonum pensylvanicum L.	Pennsylvania smartweed	POLPY	NS	0.0004	NS	NS	0.0001	NS
Portulaca oleracea L.	Common purslane	POROL	.	.	.	.	.	NS
Potentilla recta L.	Sulfur cinquefoil	PTLRC	—	—	—	.	.	.
Ranunculus abortivus L.	Smallflower buttercup	RANAB	—	—	—	.	.	—
Rumex acetosella L.	Red sorrel	RUMAA	.	.	.	—	—	—
Rumex obtusifolius L.	Broadleaf dock	RUMOB	—	—	—	.	.	—
Senecio vulgaris L.	Common groundsel	SENVU	.	.	.	.	.	.

TABLE 2. Continued.

Weed species		Bayer code	Wooster			Hoytville		
Latin name	Common name		T	R	T × R	T	R	T × R
Setaria faberi Herrm.	Giant foxtail	SETFA	0.0001	0.0008	0.0015	0.0001	0.0001	0.0001
Setaria glauca (L.) Beauv.	Yellow foxtail	SETLU	NS	0.0005	NS	NS	0.0005	NS
Silene alba (Mill.) E.H.L. Krause	White campion	MELAL	—	—	—	.	.	.
Solanum ptycanthum Dun.	Eastern black nightshade	SOLPT	.	.	.	.	.	.
Sonchus oleraceus L.	Annual sowthistle	SONOL	.	.	.	.	.	.
Stellaria media (L.) Vill.	Common chickweed	STEME	0.0377	0.0129	NS	—	—	—
Taraxacum officinale Weber in Wiggers	Dandelion	TAROF	.	.	.	—	—	—
Thlaspi arvense L.	Field pennycress	THLAR	.	.	.	—	—	—
Trifolium pratense L.	Red clover	TRFPR	.	.	.	.	.	.
Veronica arvensis L.	Corn speedwell	VERAR	0.0261	0.0001	NS	.	.	.

a "—" indicates species not present; "." indicates species not analyzed (criteria for analysis: species must appear in seedbank all 3 yr; total density >20 and total frequency >10 for at least two of those years).

earlier suggestions that the large, deep cracks formed when this clay soil dries provide channels for downward movement of weed seeds throughout the soil profile (Cardina et al. 1991).

Seed Density

For species with significant tillage effects (and no interaction with rotation), NT, CP, and MP favored different weeds (Table 3). For example, at Wooster there was a lower density of germinable seeds of common chickweed in MP plots (50 seeds m^{-2}) than in CP plots (210 seeds m^{-2}), whereas NT plots (150 seeds m^{-2}) did not differ from the other tillage treatments. The data suggest that common chickweed does not tolerate deep plowing but survives with no or moderate soil disturbance. In MP plots the densities of redroot pigweed (310 seeds m^{-2}) and corn speedwell (90 seeds m^{-2}) were both lower than in NT plots (620 and 560 seeds m^{-2}, respectively).

At Hoytville the CP tillage system favored barnyardgrass (180 seeds m^{-2}) compared with the NT (20 seeds m^{-2}) and MP (80 seeds m^{-2}) systems, which did not differ significantly (Table 3). NT plots had a higher density of yellow woodsorrel (390 seeds m^{-2}) and common lambsquarters (100 seeds m^{-2}) than did plots with the other tillage systems. These results suggest that barnyardgrass seeds do not survive well at the soil surface in NT or when incorporated deep into the soil in MP but are best adapted to moderate disturbance and some soil surface residue. The small-seeded broadleaves, common chickweed at Wooster and yellow woodsorrel and common lambsquarters at Hoytville, are likely to be incorporated into the upper surface of the soil in NT at a depth that favors successful establishment and protection from seed predators. The high density of common lambsquarters in NT compared with other tillage systems reflects the high density of seeds near the surface, where this species germinates and emerges, and might be a result of resistance to triazine herbicides used in these studies.

Relative Importance

To determine how individual species changed in response to tillage and rotation treatments, we calculated an RI index based on the relative density and relative frequency of each species in every plot. For each tillage system, species were ordered using the RI ranking in the NT plots (averaged over rotations, replications, and years); for each rotation, species were ordered using the RI ranking in the CCC plots (averaged over tillage treatments, replications, and years) (Figure 2). Although there were tillage-by-rotation interactions for seed density of some species (see earlier), we were unable to detect biologically meaningful interactions for the synthetic RI values (data not shown); therefore, averaging RI over tillage and rotation treatment provides a reasonable view of these main effects. Shifts in individual species are indicated by significant differences in RI values based on a Kruskal–Wallis test that compared the RI values for CP and MB with the values for NT, and the RI values for CS and COH with the values for CCC.

At Wooster the RI values for yellow woodsorrel, giant foxtail, henbit (*Lamium amplexicaule* L.), prickly lettuce (*Lactuca serriola* L.), and common mallow (*Malva neglecta*

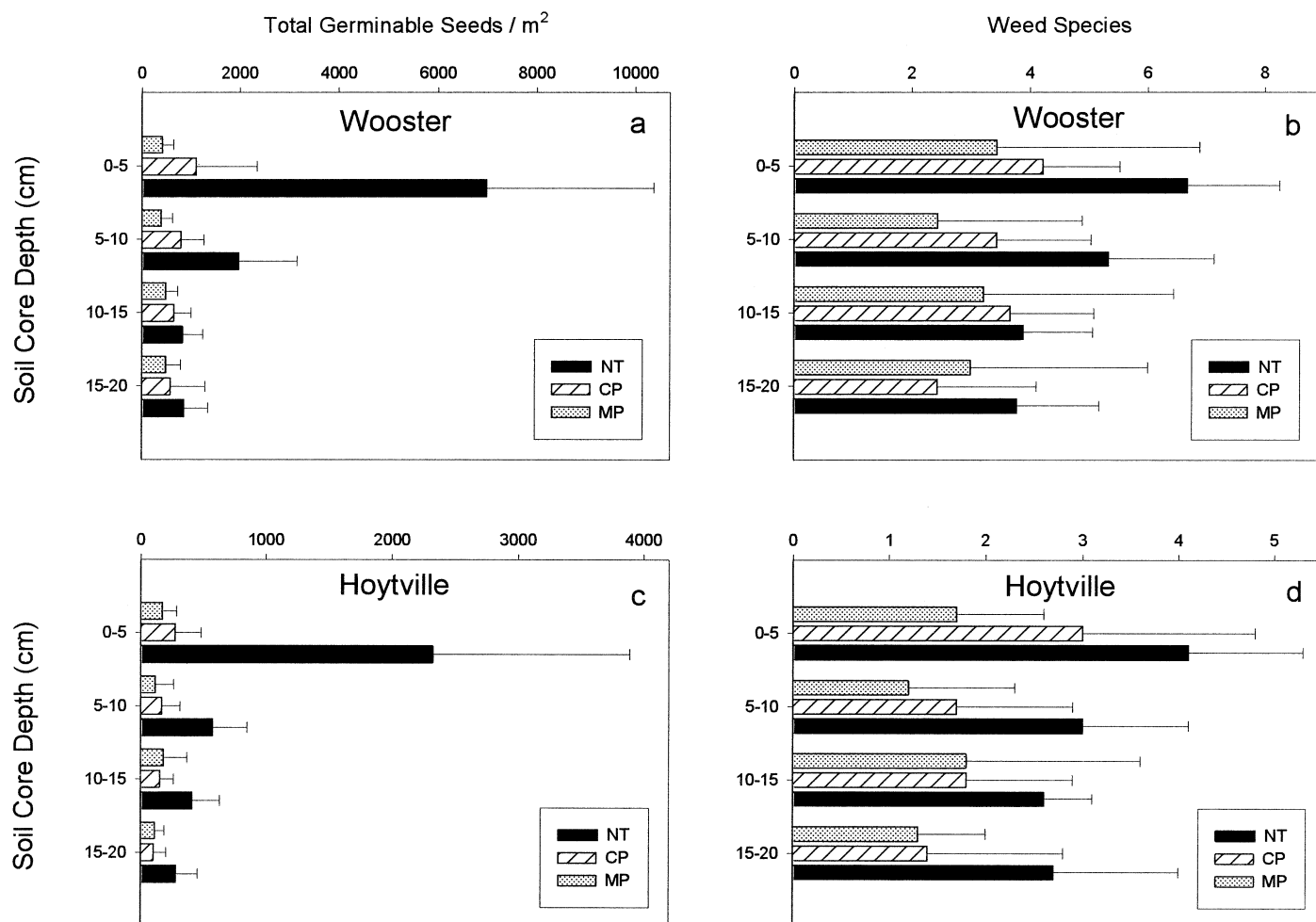Cardina et al.: Rotation, tillage, and seedbanks • 453

FIGURE 1. The number of germinable seeds (a,c) and weed species (b,d) at four soil depths in no-tillage (NT), chisel plow (CP), and moldboard plow (MP) plots after 35 yr of continuous corn at Wooster (a,b) and Hoytville (c,d). Data are means (and standard deviations) of three replications over 3 yr.

L.) were lower in CP than in NT, whereas the RI values for common chickweed, shepherd's-purse, broadleaf plantain, and annual bluegrass (*Poa annua* L.) were higher (Figure 2b). The RI values of yellow woodsorrel, giant foxtail, purple deadnettle (*Lamium purpureum* L.), and common mallow were lower in MP than in NT, whereas the RI values of large crabgrass, annual fleabane [*Erigeron annuus* (L.) Pers.], shepherd's-purse, broadleaf plantain, annual bluegrass, and common purslane (*Portulaca oleracea* L.) were higher (Figure 2c). At Hoytville the five species with the highest RI in NT (giant foxtail, redroot pigweed, yellow woodsorrel, large crabgrass, and Pennsylvania smartweed) did not change in importance in CP or MP (Figures 2d–f.) In both CP and MP the RI of yellow foxtail and barnyardgrass was 160 to over 400% higher than that in NT, whereas the RI of common lambsquarters was 54% lower in MP than in NT.

These results support the general interpretation of Zanin et al. (1997) regarding the increased importance of specific annuals whose survival is linked to disturbance in MP, although we did not find the clear trend toward vegetatively propagated species in NT that they described. The Wooster data show that common lambsquarters was dominant in all tillage systems. As soil disturbance increased, the importance of several other species (especially shepherd's-purse, broadleaf plantain, and annual bluegrass) increased to fill the

niches made available by tillage and by the decline in yellow woodsorrel, giant foxtail, and common mallow.

Main Effects of Rotation

Seed Density

Densities of several species differed significantly among crop rotations irrespective of tillage system (Table 4). At both locations large crabgrass was consistently more abundant (300 to 550 seeds m^{-2}) in the three-crop COH rotation than in the other rotations (40 to 310 seeds m^{-2}). At Wooster fall panicum and yellow foxtail followed this same pattern, but at Hoytville seed density of yellow foxtail differed only in COH (610 seeds m^{-2}) and CS (20 seeds m^{-2}) plots. In contrast, fall panicum at Hoytville was more abundant in CCC (230 seeds m^{-2}) than in CS (10 seeds m^{-2}) and COH (40 seeds m^{-2}). Fall panicum germinates relatively late and is fairly tolerant of triazine herbicides, which might account for its increase in CCC (Triplett and Lytle 1972). The reasons why the other grasses were consistently favored by the three-crop rotation are likely related to their adaptation to the hay or oats component of the rotation. Large crabgrass, for example, has a decumbent growth habit and tolerates mowing; yellow foxtail and barnyardgrass are fairly common weeds of hay in Ohio. Contrary results were

TABLE 3. Effect of tillage system on seed density (to 10-cm depth) of the species for which there were no interactions with rotation or year at Wooster and Hoytville. Data are means (and standard deviations) of six rotation treatments, three replications, and three sampling years.[a]

Till-age[b]	Wooster			Hoytville		
	AMARE	STEME	VERAR	ECHCG	OXAST	CHEAL
	seeds m^{-2}					
NT	620 a	150 ab	560 a	20 b	390 a	100 a
	(720)	(210)	(720)	(40)	(410)	(100)
CP	490 ab	210 a	330 ab	180 a	150 b	40 b
	(490)	(160)	(550)	(220)	(230)	(50)
MP	310 b	50 b	90 b	80 b	10 c	40 b
	(630)	(80)	(130)	(120)	(30)	(100)

[a] Means within a column followed by the same letter do not differ at the 0.05 significance level according to the analysis of variance F-test.
[b] Abbreviations: NT, no-tillage; CP, chisel plowing; MP, moldboard plowing.

reported by Schreiber (1992), who found that crop rotations including a small grain decreased foxtail populations compared with those in CCC.

Three broadleaves at Wooster (shepherd's-purse, Pennsylvania smartweed, and corn speedwell) and four at Hoytville (yellow woodsorrel, redroot pigweed, Pennsylvania smartweed, and spotted spurge) were more abundant in the COH rotation (260 to 630 seeds m^{-2}) than in CS (10 to 270 seeds m^{-2}) or CCC (< 1 to 60 m^{-2}), regardless of the tillage system (Table 4). At Wooster common chickweed was more abundant in COH (200 seeds m^{-2}) than in CCC (40 seeds m^{-2}). The increased abundance of broadleaves in the COH rotation is likely the result of several factors, one being that fewer herbicides were applied to the hay or oats crops than to the corn and soybean crops. Over the last 9 yr, about 106 kg ha^{-1} of herbicides were applied to the COH plots (92 kg of this to corn) compared with 275 kg ha^{-1} to the CCC and 214 ha^{-1} to the CS rotation plots. Because oats were generally planted in March, corn in May, and hay in August, the three-crop rotation plots provided an environment favorable to weeds adapted to germination and establishment at different times in the growing season. Pennsylvania smartweed at both locations was strongly favored by COH (260 and 630 seeds m^{-2}) compared with CCC (10 and 20 seeds m^{-2}) and CS (10 and 50 seeds m^{-2}) rotations, possibly because of the ability of this species to regrow after oats and hay cuttings. At Wooster shepherd's-purse density was higher (580 seeds m^{-2}) in COH than in CCC and CS (10 seeds m^{-2}), probably because of the ability to germinate in fall or spring in Ohio. At Hoytville spotted spurge was more abundant in COH (140 seeds m^{-2}) than in CCC (< 1 seed m^{-2}) and CS (10 seeds m^{-2}) rotations because of its tolerance of corn and soybean herbicides and its adaptation to summer germination in oats stubble and hay. Corn speedwell was more abundant at Wooster in COH (580 seeds m^{-2}) than in CC (110 seeds m^{-2}) and CS (270 seeds m^{-2}) because of its adaptation to mowing. Redroot pigweed did not differ among rotation treatments at Wooster, but at Hoytville it was strongly favored by COH (570 seeds m^{-2}) over CCC (50 seeds m^{-2}) and CS (70 seeds m^{-2}).

These results suggest specific cultural practices that might mitigate infestations of particular weeds. For example, management of fall panicum infestations in CCC might be re-

duced by rotation to soybean or to oats and hay crops. Yellow woodsorrel might be suppressed by MP and corn or soybean production. Common chickweed, an important problem weed in Ohio forage seedings, might be suppressed by plowing and a few years of corn production (Loux and Berry 1991). A challenge for managers is to anticipate how such changes in tillage or rotation are likely to favor other weeds in order to avoid shifts to other troublesome species.

Relative Importance

Species shifts were evident among crop rotations at Wooster, with lower RI values for common lambsquarters, redroot pigweed, nimblewill (*Muhlenbergia schreberi* J.F. Gmel.), yellow foxtail, purple deadnettle, and yellow nutsedge (*Cyperus esculentus* L.) in the CS than in the CCC plots (Figure 3b). Species shifts were more marked in the COH rotation where the RI values for common lambsquarters and redroot pigweed were 88 and 29% lower, respectively, compared with CCC, whereas there were relatively large increases in RI of yellow woodsorrel (497%), purple deadnettle (83%), annual sowthistle (*Sonchus oleraceus* L.) (150%), yellow nutsedge (90%), common groundsel (*Senecio vulgaris* L.) (140%), annual fleabane (270%), and corn speedwell (444%) (Figure 3c). Species whose RI values increased in the three-crop rotation were mostly winter annuals or perennials whose seed production and survival are apparently favored by conditions in oats and hay crops compared with conditions in CCC.

At Hoytville the RI value of giant foxtail was 80% lower in COH than in CCC, whereas RI values of large crabgrass and eastern black nightshade (*Solanum ptycanthum* Dun.) were 18 to 76% higher in CS and COH rotations than in CCC (Figures 3d–f). No seeds of spotted spurge were found in CCC at Hoytville, but the RI of this species in COH (0.04) was equivalent to the RI of the fourth and fifth most important species (redroot pigweed and common lambsquarters) in CCC.

Tillage-by-rotation Interactions

There was a significant interaction between tillage and rotation for fall panicum, giant foxtail, common lambsquarters, and yellow woodsorrel at Wooster, as well as for giant foxtail at Hoytville (Table 5). In addition, the interaction was significant for total seed density at both locations. At Wooster the differences in grass density among rotations were dependent on the tillage system. In NT, for example, fall panicum density was higher in CCC (3,750 seeds m^{-2}) than in CS and COH (2,560 and 820 seeds m^{-2}, respectively), whereas in MP seed density was higher in COH (480 seeds m^{-2}) than in CCC (< 10 seeds m^{-2}) or CS (100 seeds m^{-2}). In the CP plots there were no differences in the density of fall panicum among rotations. This suggests that this species is particularly well suited to the NT corn environment and persists best in MP where oats and hay are included in the rotation. The characteristics that make this species better adapted to NT corn than to tilled or chiseled corn, or to other rotations, might include its late germination and late seed maturation that coincides well with corn harvest. Characteristics of the NT corn environment that favor fall panicum include a high amount of surface residue, which interferes with herbicide movement into the soil and

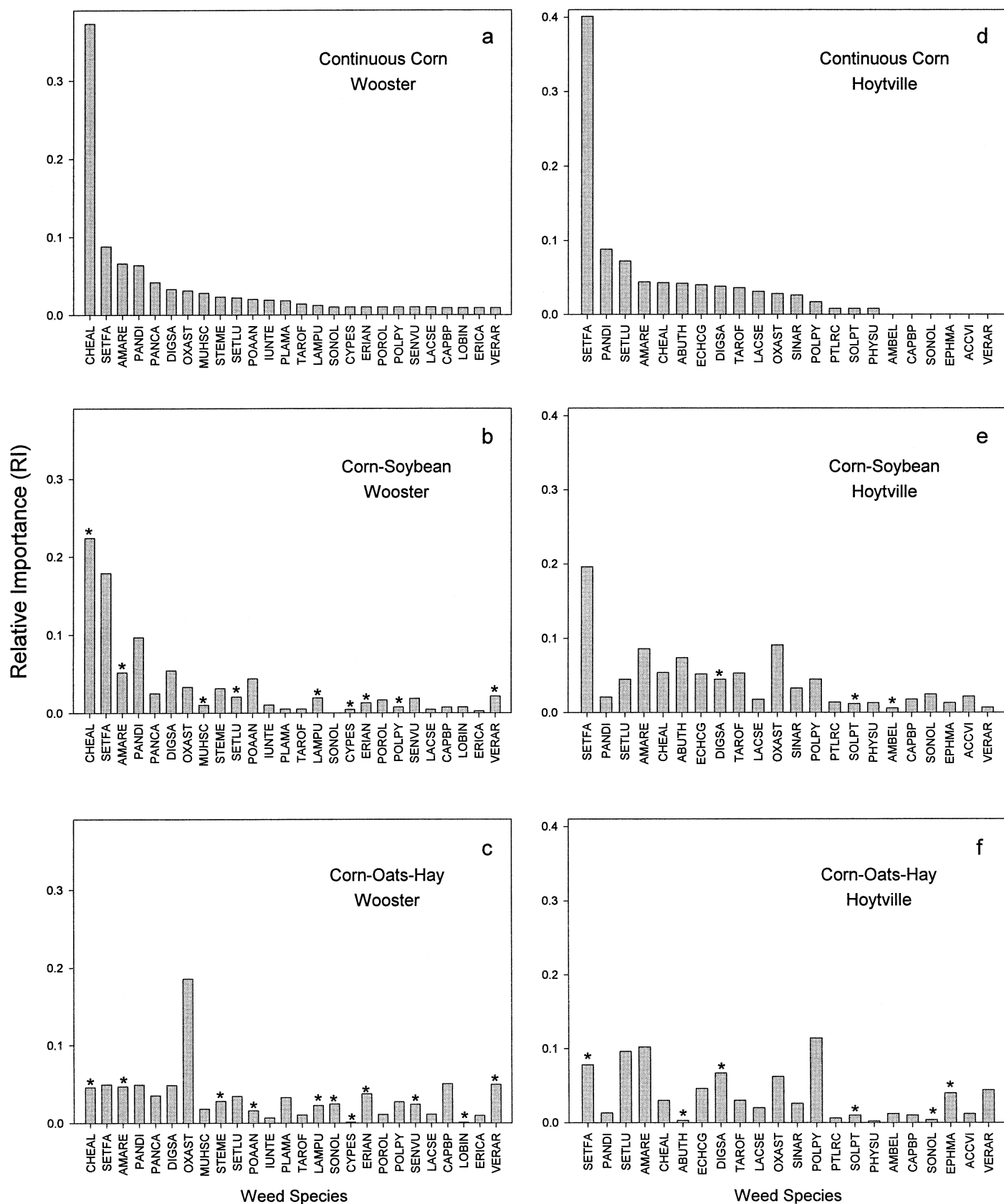Cardina et al.: Rotation, tillage, and seedbanks • 455

FIGURE 2. Relative importance (RI) index values for selected species in no-tillage (NT), chisel plow (CP), and moldboard plow (MP) plots after 35 yr at Wooster (a–c) and Hoytville (d–f). Data are averaged over three replications and 3 yr of three crop rotations. Species are ordered according to their rank in NT, and asterisks (*) indicate significant differences between RI values in NT and CP or MP.

TABLE 4. Effect of crop rotation on seed density (to 10-cm depth) of the species for which there were no interactions among tillage, rotation, and year at Wooster and Hoytville. Data are means (and standard deviations) of three replications, three tillage systems, and three sampling years.[a]

Crop rotation[b]	Grass weeds				Broadleaf weeds			
					seeds m^{-2}			
Wooster	DIGSA	PANDI	SETLU		STEME	CAPBP	POPLY	VERAR
CCC	60 b	120 b	210 b		40 b	20 b	10 b	10 b
	(50)	(120)	(570)		(30)	(40)	(20)	(20)
CS	310 b	80 b	50 b		100 ab	10 b	10 b	270 b
	(370)	(140)	(60)		(130)	(30)	(30)	(160)
COH	550 a	280 a	320 a		200 a	580 a	260 a	580 a
	(490)	(260)	(420)		(190)	(420)	(450)	(680)
Hoytville	DIGSA	PANDI	SETLU	ECHCG	OXAST	AMARE	POLPY	EPHMA
CCC	60 b	230 a	200 ab	70 ab	50 b	60 b	20 b	< 10 b
	(110)	(180)	(310)	(130)	(70)	(75)	(60)	(10)
CS	40 b	10 b	20 b	30 b	100 b	70 b	50 b	10 b
	(80)	(40)	(30)	(30)	(140)	(98)	(200)	(30)
COH	300 a	40 b	610 a	150 a	290 a	570 a	630 a	140 a
	(340)	(70)	(1080)	(190)	(460)	(665)	(740)	(150)

[a] Means within a column and within a location followed by the same letter do not differ at the 0.05 significance level according to the ANOVA F-test.
[b] Abbreviations: CCC, continuous corn; CS, corn–soybean; COH, corn–oats–hay.

keeps soil moisture near the surface. These characteristics allow fall panicum to germinate later in the growing season than might be the case in tilled systems that leave less surface residue. The reason why this species persists in COH better than in CCC or CS in an MP system is unclear; however, of the three rotations, COH maintains the most surface cover and soil organic matter when the soil is MP (Dick and VanDoren 1985).

At Wooster giant foxtail seed density followed a pattern similar to that of fall panicum (Table 5). In NT giant foxtail seed density was lower in COH (920 seeds m^{-2}) than in CCC and CS (3,920 and 6,890 seeds m^{-2}, respectively), whereas in MP seed density was lower in CCC (20 seeds m^{-2}) than in CS and COH (220 and 240 seeds m^{-2}, respectively). For plots that were CP, giant foxtail seed density did not differ among crop rotations. However, single degree-of-freedom contrasts showed that when averaged over rotation treatments, giant foxtail was more abundant in NT (3,370 seeds m^{-2}) than in CP (620 seeds m^{-2}) or MP (200 seeds m^{-2}). When averaged over tillage treatments, giant foxtail was more abundant in the CS rotation (2,650 seeds m^{-2}) than in CCC and COH (1,350 and 590 seeds m^{-2}, respectively) (data not shown). In MP soil-applied grass herbicides perform better, and corn emerges earlier than in NT; therefore, early competition from corn is likely greater in MP than in NT. In an MP-COH system where the clover (*Trifolium* spp.) is incorporated into the soil before planting, more N is likely available to the emerging giant foxtail than in NT systems where the clover crop is simply killed with a nonselective herbicide. The greater abundance of giant foxtail seeds in the CS rotation plots reflects possible resource partitioning between soybean and grass weeds as well as generally poorer grass control in soybean than in other crops.

The interaction among tillage and rotation treatments for giant foxtail seed density at Hoytville was somewhat different from that at Wooster (Table 5). Seed abundance in NT was higher in CCC (6,890 seeds m^{-2}) than in the other rotations (530 seeds m^{-2}), whereas seed abundance in CP

was higher in COH (520 seeds m^{-2}) than in CCC and CS (330 and 160 seeds m^{-2}, respectively), and seed abundance in MP did not differ among rotations. Averaged over rotation treatments, giant foxtail seeds were significantly more abundant in NT (1,580 seeds m^{-2}) than in CP (370 seeds m^{-2}), which was significantly different from MP (150 seeds m^{-2}) (contrasts not shown). Averaged over tillage systems, giant foxtail density was higher in CCC (2,440 seeds m^{-2}) than in CS and COH (400 and 440 seeds m^{-2}, respectively). The dominance of giant foxtail in the seedbank of continuous NT corn plots in these experiments is consistent with the experience of growers throughout Ohio (Loux and Berry 1991).

At both locations there was a significant interaction between tillage and rotation for estimates of the total seed density (Table 5). The highest seed density was in NT-CCC, with 26,850 seeds m^{-2} at Wooster and 8,680 seeds m^{-2} at Hoytville. At Wooster total seed density in CCC plots was 45 and 60% lower than in COH plots for CP and MP, respectively. However, in NT plots the total seed density was 40% greater in CCC than in COH. At Hoytville the pattern was similar, with the total seed density in CCC plots 72% lower than in COH plots that were CP or MP, whereas seed density was 45% greater in CCC than in COH plots that were in an NT system. Single–degree of freedom contrasts (not shown) indicated that total seed density at Hoytville was consistently lower ($\bar{x}$ = 860 seeds m^{-2}) in CS than in CCC ($\bar{x}$ = 3,620 seeds m^{-2}) and COH ($\bar{x}$ = 4,230 seeds m^{-2}). For CCC and CS rotations, seed density was consistently greater in NT than in the corresponding rotation plots that were CP or MP. This suggests that the relatively undisturbed soil surface environment in continuous NT corn favors weed seed production and survival, whereas the soil environment in COH rotations favors those processes where soil is disturbed annually by a moldboard or chisel plow.

As the dominance of giant foxtail decreased with more complex crop rotation and greater soil disturbance, suitable niches were occupied by other species. This suggests that
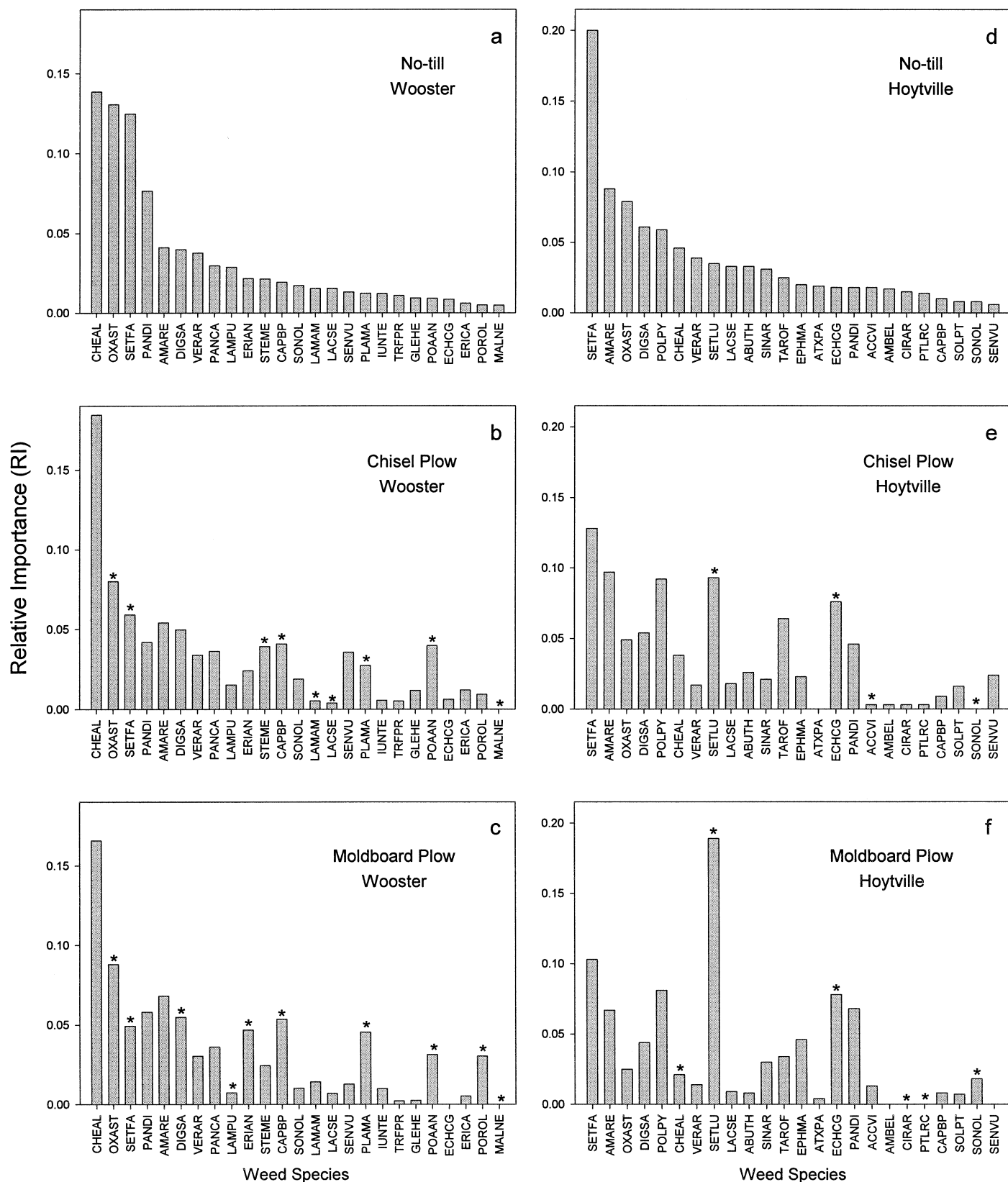
Cardina et al.: Rotation, tillage, and seedbanks • 457

FIGURE 3. Relative importance (RI) index values for selected species in continuous corn (CCC), corn–soybean (CS), and corn–oats–hay (COH) rotations after 35 yr at Wooster (a–c) and Hoytville (d–f). Data are averaged over three replications and 3 yr of three tillage systems. Species are ordered according to their rank in CCC, and asterisks (*) indicate significant differences between RI values in CCC and CS or COH.

TABLE 5. Effect of tillage system and crop rotation on seed density (up to 10-cm depth) of grass and broadleaf species for which there were significant tillage-by-rotation interactions at Wooster and Hoytville. Data are means (and standard deviations) of three replications and three sampling years.[a]

		Wooster					Hoytville	
Tillage[b]	Rotation[c]	PANDI	SETFA	CHEAL	OXAST	TOTAL	SETFA	TOTAL
		seeds m^{-2}						
NT	CCC	3,750 a (5,310)	3,920 a (3,360)	17,880 a (6,650)	500 cd (260)	26,850 a (10,070)	6,830 a (900)	8,680 a (1,000)
	CS	2,560 b (1,680)	6,890 a (5,570)	2,690 c (2,290)	290 de (210)	15,980 bc (8,850)	530 bc (590)	1,670 d (570)
	COH	820 b (1,160)	920 b (580)	510 e (410)	7,250 a (3,100)	16,340 b (8,850)	530 bc (560)	4,770 b (1,780)
CP	CCC	160 bcd (90)	210 cd (180)	3,780 bc (790)	20 ef (30)	5,670 d (950)	330 bc (120)	1,310 d (180)
	CS	130 cd (100)	830 bc (850)	6,090 b (2,580)	90 ef (160)	9,360 c (340)	160 cd (170)	540 ef (330)
	COH	460 bc (490)	610 cd (860)	440 e (310)	2,150 b (830)	10,300 c (2,420)	520 b (420)	4,800 b (1,750)
MP	CCC	< 10 d (10)	20 e (30)	1,550 cd (1,190)	20 ef (30)	2,360 e (1,150)	190 bcd (200)	870 de (470)
	CS	100 c (110)	220 d (290)	1,550 cd (570)	30 e (30)	2,650 e (930)	80 d (140)	370 f (160)
	COH	480 b (600)	240 d (210)	640 de (370)	1,040 c (880)	5,870 d (1,990)	170 cd (200)	3,120 c (1,900)

[a] Means within a column followed by the same letter do not differ at the 0.05 significance level according to the LSD.
[b] Abbreviations: NT, no-tillage; CP, chisel plowing; MP, moldboard plowing.
[c] Abbreviations: CCC, continuous corn; CS, corn–soybean; COH, corn–oats–hay.

there might be a finite number of sites that can be occupied by species with generally similar requirements for growth and survival. Thus, a decline in the occurrence of one species might leave resources available for other species with a marginally better tolerance of microenvironmental conditions or a greater ability to acquire resources provided by different tillage and rotation systems. This suggests that it would be easier to manage weeds in continuous NT corn than in other tillage systems or more complex crop rotations where a single species dominates, and herbicides are available to manage that species. However, replacement of a dominant species like giant foxtail with species such as yellow woodsorrel or corn speedwell, which would be expected to have less effect on the crop compared with giant foxtail, might decrease the overall effect of weeds even though all available niches are filled. If this speculation holds, then manipulations of rotation, tillage, and other cultural practices might be found that allow all available niches to be filled by species that have little effect on the crop.

The results of this study can be applied in a "community assembly" context to help understand how particular assemblages of weeds arise or decline and how cropping systems can be better managed to reduce the effect of weeds (Drake et al. 1999). Our data suggest that management practices, such as tillage, rotations, and herbicides, act as filters that determine the composition and abundance of weed species in crop fields. These management practices filter out specific plant characteristics to determine the trajectory of community change. The plant characteristics that result in a species being maintained in or filtered out of the community are often unknown but might include seed physical properties (size, shape, dispersal adaptations) or physiological traits (dormancy type, germination requirements, longevity). The filtering mechanism might involve dispersal, environmental,

or internal constraints (Belyea and Lancaster 1999). For example, Doucet et al. (1999) concluded that weed management method was a more important environmental filter than crop rotation in determining weed density and diversity. Our results suggest that rotation and tillage are both important environmental filters and that these factors often interact to determine the abundance and composition of seeds in the soil seedbank. The seedbank, then, is both a cause and a result of the existing vegetation, reflecting past and current management while providing a picture of potential future vegetation.

Sources of Materials

Acknowledgments

Literature Cited

Ball, D. A. 1992. Weed seedbank response to tillage, herbicides, and crop rotation sequence. Weed Sci. 40:654–659.
Ball, D. A. and S. D. Miller. 1990. Weed seed population response to tillage and herbicide use in three irrigated cropping sequences. Weed Sci. 38:511–517.

Barberi, P., A. Cozzani, M. Macchia, and E. Bonari. 1998. Size and composition of the weed seedbank under different management systems for continuous maize cropping. Weed Res. 38:319–334.

Belyea, L. R. and J. Lancaster. 1999. Assembly rules within a contingent ecology. Oikos 86:402–416.

Buhler, D. D. 1995. Influence of tillage system on weed population dynamics and management in corn and soybean in the central USA. Crop Sci. 35:1247–1258.

Cardina, J., E. Regnier, and K. Harrison. 1991. Long-term tillage effects on seedbanks in three Ohio soils. Weed Sci. 39:186–194.

Cardina, J. and D. H. Sparrow. 1996. A comparison of methods to predict weed seedling populations from the soil seedbank. Weed Sci. 44:46–51.

Derksen, D. A., A. G. Thomas, G. P. Laford, H. A. Loeppky, and C. J. Swanton. 1994. Impact of agronomic practices on weed communities: fallow within tillage systems. Weed Sci. 42:184–194.

Dick, W. A. and C. T. Daniel. 1987. Soil chemical and biological properties as affected by conservation tillage: environmental implications. Pages 124–147 in T. J. Logan, J. M. Davidson, J. L. Baker, and M. R. Overcash, eds. Effects of Conservation Tillage on Groundwater Quality. Chelsea, MI: Lewis Publishers.

Dick, W. A. and D. M. Van Doren, Jr. 1985. Continuous tillage and rotation combinations effects on corn, soybean, and oat yields. Agron. J. 77:459–465.

Dick, W. A., D. M. Van Doren, Jr., G. B. Triplett, Jr., and J. E. Henry. 1986. Influence of long-term tillage and rotation combinations on crop yields and selected soil parameters. II. Results obtained for a Typic Fragiudalf soil. Ohio State Univ. Res. Bull. 1181:34 p.

Dorado, J., J. P. Del Monte, and C. Lopez-Fando. 1999. Weed seedbank response to crop rotation and tillage in semiarid agroecosystems. Weed Sci. 47:67–73.

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

Drake, J. A., C. R. Zimmermann, T. Prurcker, and C. Rojo. 1999. On the nature of the assembly trajectory. Pages 233–250 in E. Weir and P. A. Keddy, eds. Ecological Assembly Rules: Perspectives, Advances, Retreats. Cambridge, Great Britain: Cambridge University Press.

Forcella, F., R. G. Wilson, K. A. Renner, J. Dekker, R. G. Harvey, D. A. Alm, D. D. Buhler, and J. Cardina. 1992. Weed seedbanks of the U.S. Corn Belt: magnitude, variation, emergence, and application. Weed Sci. 40:636–644.

Huynh, H. and L. S. Feldt. 1970. Conditions under which mean square ratios in repeated measurements designs have exact F-distributions. J. Am. Stat. Assoc. 65:1582–1589.

Kremer, R. J. 1993. Management of weed seed banks with microorganisms. Ecol. Appl. 3:42–52.

Liebman, M. and E. Dyck. 1993. Crop rotation and intercropping strategies for weed management. Ecol. Appl. 3:92–122.

Loux, M. M. and M. A. Berry. 1991. Use of a grower survey for estimating weed problems. Weed Technol. 5:460–466.

Martin, R. J. and W. L. Felton. 1993. Effect of crop rotation, tillage practice, and herbicides on the population dynamics of wild oats in wheat. Aust. J. Exp. Agric. 33:159–165.

Schreiber, M. 1992. Influence of tillage, crop rotation, and weed management on giant foxtail (Setaria faberi) population dynamics and corn yield. Weed Sci. 40:645–653.

Steel, R.G.D. and J. H. Torrie. 1980. Principles and Procedures of Statistics: A Biometrical Approach. New York: Mcgraw-Hill. pp. 544–545.

Thompson, K. and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Appl. Ecol. 67:893–921.

Triplett, G. B., Jr. and G. D. Lytle. 1972. Control and ecology of weeds in continuous corn without tillage. Weed Sci. 20:453–457.

Wicks, G. A., O. C. Burnside, and W. L. Felton. 1994. Weed control in conservation tillage systems. Pages 211–244 in P. W. Unger, ed. Managing Agricultural Residues. Boca Raton, FL: Lewis Publishers.

Yenish, J. P., J. D. Doll, and D. D. Buhler. 1992. Effects of tillage on vertical distribution and viability of weed seed in soil. Weed Sci. 40:429–433.

Zanin, G., S. Otto, L. Riello, and M. Borin. 1997. Ecological interpretation of weed flora dynamics under different tillage systems. Agric. Ecosyst. Environ. 66:177–188.