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## Cropping system effects on giant foxtail (*Setaria faberi*) demography: I. Green manure and tillage timing

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Manipulation of cropping systems to improve weed management requires a better understanding of how crop- and soil-related factors affect weed life cycles. Our objective was to assess the impacts of timing of primary tillage and use of legume green manure on giant foxtail demography and soil properties. We measured giant foxtail seed survival and dormancy, seedling emergence and survival, and fecundity, in addition to soil phytotoxicity, chemical properties affecting soil fertility and soil water, in the transition between the wheat and corn phases of a wheat–corn–soybean crop sequence. Postdispersal predation of giant foxtail seeds was measured in all three phases of the crop sequence. Wheat was grown either as a sole crop (W) or underseeded with red clover (R), and residues from this phase were rototilled either in the fall (FT) or in spring (ST). There were strong interactions between Red clover and Tillage timing in their effects on giant foxtail recruitment and fecundity in corn. Giant foxtail seedling emergence was 30% lower, and time to 50% emergence was more than 1 wk later, in the ST/R treatment than in the ST/W, FT/W, and FT/R treatments, which did not differ. However, fecundity of giant foxtail was 200% greater in the ST/R treatment than in the other three treatments because of suppressed early corn growth. The net effect of the ST/R treatment on giant foxtail demography in corn was to greatly increase inputs to the seedbank compared with the ST/W, FT/W, and FT/R treatments. Giant foxtail demography in the wheat phase was also affected by Red clover. There was a 200% increase in daily rates of postdispersal seed predation in the wheat phase of the R treatment compared with the W treatment. High-seed predation in the wheat phase and low fecundity in the corn phase of the FT/R treatment suggest that population growth rate of giant foxtail will be lower in this treatment than in the other treatments. The degree of soil phytotoxicity from red clover residues, the changes in the amount of interference from the corn crop early in the growing season, and the differential suitability of crop residues in the different rotations as habitat for seed predators all contributed to changes in giant foxtail demography. Understanding the effects of cropping system characteristics on entire weed life cycles will facilitate the design of integrated suites of complementary weed management tactics.

**Nomenclature:** Giant foxtail, *Setaria faberi* Herrm. SETFA; corn, *Zea mays* L. 'Pioneer 3512'; red clover, *Trifolium pratense* L. 'Cherokee'; soybean, *Glycine max* (L.) Merr. 'IA 2039'; spring wheat, *Triticum aestivum* L. 'Sharp'.

**Key words:** Soil organic amendments, allelopathy, integrated weed management, postdispersal seed predation, arthropod activity-density, seedbank dynamics, dormancy, seedling recruitment, fecundity.

A key priority for integrated weed management research should be to identify cropping system characteristics that prevent weed population growth without sacrificing crop performance (Jordan 1996). This is an especially important goal in low-external-input (LEI) systems, where intensive herbicide use is not an option (Liebman and Davis 2000). Crop sequence, cultivar choice, tillage regime, use of soil organic amendments, and other cropping system characteristics can strongly influence weed population densities (Buhler 1995; Buhler et al. 2001; Gallandt et al. 1998). Although producers normally would not base their choice of cropping system entirely on its weed management merits, an increased understanding of cropping system effects on weed demography will enable a more informed choice of such systems (Buhler 2002).

Two areas of limited knowledge hinder the intentional use of cropping systems to prevent the buildup of weed populations. First, whole weed life cycles are rarely the unit

of study. Despite the proliferation of dynamic models that simulate management effects on weed populations (Blumenthal and Jordan 2001; Bussan and Boerboom 2001a, 2001b; Gonzalez-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995; Lindquist et al. 1995; Pino et al. 1998; Shea and Kelly 1998), there are few empirical studies of management effects on entire weed life cycles (Cousens and Mortimer 1995) and even fewer that are focused on weed life cycles in LEI systems (Misra et al. 1992; Ullrich 2000). Because weed life history traits often are highly variable in temporal (Burnside et al. 1996; Forcella et al. 1997), climatological (Benech-Arnold et al. 2000; Ullrich 2000; Weaver et al. 1988), and genetic (Rice and Mack 1991; Wang et al. 1995) dimensions, it may be difficult to assess reliably how management effects on individual demographic rates contribute to changes in weed population growth rate when parameter estimates are pooled from different study

sites, years, and populations. More unified demographic data sets will aid weed population management.

A second area of limited knowledge is how agronomic practices affect ecological determinants of weed population dynamics. This literature is small, but growing (Arntz et al. 2000; Dekker and Hargrove 2002; Teasdale and Mohler 2000; Weaver et al. 1988). Few studies, however, link ecological effects of management practices to weed population ecology (Buhler and Mester 1991; Menalled et al. 2000; Ullrich 2000).

Demographic studies of individual weed species are a practical starting place for identifying cropping system characteristics with weed management potential. To increase the general utility of such results, a logical next step would be to conduct multispecies experiments (with interspecific variation relevant to the domain of inference) using the most promising management systems. Giant foxtail was chosen as a model species for the first stage in this process for several reasons. First, giant foxtail is a widespread, economically important summer annual weed of the north-central U.S. corn belt (Lindquist et al. 1999). Second, considerable biological information already exists for giant foxtail (Buhler and Hartzler 2001; Bussan and Boerboom 2001a; Dekker and Hargrove 2002; Fausey and Renner 1997; Forcella et al. 1997; Mester and Buhler 1991), facilitating the design and interpretation of this study. Third, the annual life history and ephemeral seedbank of giant foxtail (Buhler and Hartzler 2001) allowed us to avoid the complexity of age- and stage-structured populations (Caswell 2001). Finally, low genetic diversity in giant foxtail populations (Wang et al. 1995) minimized variability that could obscure management effects on demography.

In previous work (Conklin et al. 2002; Davis and Liebman 2001), reduced wild mustard growth and interference were observed in sweet corn grown in soil amended with a red clover green manure and composted dairy manure compared with sweet corn grown without organic amendments but fertilized with synthetic N. Bioassays showed less weed suppression with increasing time after amendment incorporation (Conklin et al. 2002), indicating that tillage timing may modify soil amendment effects on weeds.

The objective of the present study was to assess the effects of wheat–red clover green manure and tillage timing on soil properties and giant foxtail demography in corn. Crop diversification in Iowa is likely to build upon a corn–soybean crop sequence, therefore we placed our study within the context of a wheat–corn–soybean crop sequence. We tested two hypotheses. First, we predicted that wheat underseeded with red clover in a wheat–corn–soybean crop sequence would affect negatively all giant foxtail life stages in the corn phase. The rationale for this hypothesis was that if phytotoxins and pathogens associated with a red clover green manure can reduce weed seedling recruitment and growth, as mentioned above, then red clover residues may also reduce weed seed survival (as a result of increased seed decay) and fecundity (as a result of limited weed growth). Second, we predicted that time of red clover incorporation would modify residue-mediated suppression of giant foxtail life-stage transitions, with more recently incorporated residues exerting a greater suppressive effect. The rationale for this hypothesis was that phytotoxic effects of plant residues tend

to decrease with increasing time for degradation in the soil (Breland 1996; Dabney et al. 1996).

## Materials and Methods

### Field Procedures

Tillage timing and green manure effects on giant foxtail demographic rates and soil properties were measured in the transition between the wheat and corn phases of a wheat–corn–soybean crop sequence at the Iowa State University Agronomy and Agricultural Engineering Farm in Boone, IA. All entry points of the crop sequence were initiated in 1999 and again in 2000 and 2001 so that there were wheat to corn transition environments for study over multiple years. Before 1999, the experimental site had been in a conventionally managed corn–soybean crop rotation for 5 yr. Soil type was a Nicollet clay loam (Aquic Hapludolls), with 35% sand, 45% silt, 30% clay, a pH of 6.3, and 4.7% soil organic carbon (SOC).

The experiment was performed in a split-plot design with four replications. The main-plot variable was Tillage timing (fall vs. spring), and the subplot variable was Red clover (red clover present or absent in wheat phase). Main plots were 3.8 m wide by 12.2 m long and were subdivided into two 3.8-m-wide by 6.1-m-long subplots (the experimental unit of the study).

Wheat, corn, and soybean entry points of the crop sequence were established as follows. Spring wheat was grown either as a sole crop (W) or underseeded with red clover (R) as a green manure for the following corn crop. In late March of 1999, 2000, and 2001, wheat was drilled in 17.8-cm rows at 112 kg ha<sup>-1</sup>, and red clover, preinoculated with *Rhizobium*, was broadcast over subplots in the R treatment with a push-spreader at 16.8 kg ha<sup>-1</sup>. At the time of wheat planting, urea was broadcast at 60 kg N ha<sup>-1</sup>. Corn was planted on April 27 on 0.76-m-wide rows at 64,500 seeds ha<sup>-1</sup> in 1999 and 2000. This procedure was modified in 2001, so that corn was planted on April 27 at 72,000 seeds ha<sup>-1</sup> and then thinned on May 15 to a common density of 64,500 plants ha<sup>-1</sup>. Urea was banded 2.5 cm from the corn row at 90 kg N ha<sup>-1</sup> on June 5 in each study year. Soybean was planted in 0.76-m-wide rows at 395,000 seeds ha<sup>-1</sup> in 1999, 2000, and 2001. Soil tests in all years indicated that P and K levels were sufficient for wheat, corn, and soybean production (Voss et al. 1999), so P and K fertilizers were not applied.

In late October of 1999 and 2000, compost was spread on subplots transitioning from the wheat to the corn phase at 25,000 kg C ha<sup>-1</sup> (compost dry-weight C content was 11% in 1999 and 15% in 2000). Compost was obtained from a deep-bedded swine production system maintained at the Iowa State University Rhodes Research Farm (Honeyman and Kent 2001) and was aged for 6 mo before application. After compost application in late October, subplots assigned to the fall tillage treatment (FT) were tilled to a depth of 20 cm with a power takeoff–driven rototiller; subplots assigned to spring tillage (ST) were tilled in mid-April.

### Recruitment, Growth, Fecundity, and Survival

Giant foxtail recruitment, growth, fecundity, and survival were measured in the period from the end of the wheat

phase to the end of the corn phase. Postdispersal predation of giant foxtail seeds was measured in all phases of the crop sequence. Giant foxtail seeds were planted in two different ways to examine different life stages. Precise measurements of seedbank parameters including seed survival, dormancy, and recruitment were obtained with synthetic seedbanks. These consisted of 7.5-cm lengths of polyvinyl chloride (PVC) pipe, 30.5 cm in diameter, driven into the soil, to which giant foxtail seeds were added at 5,480 seeds  $m^{-2}$ . To observe plant survival, growth, and fecundity, we planted after-ripened seeds (see below) at 50 seeds  $m^{-2}$  in rows parallel to, and offset 4 cm from, the corn row on April 28 in 2000 and 2001 (referred to hereafter as row-plantings).

### Seedbank Dynamics

Ambient weed seedbank density was estimated in April 1999 by collecting thirty 2.5-cm-diam soil cores to a depth of 20 cm from each experimental unit and then sieving and washing soil to recover seeds. No giant foxtail seeds were found at the site. Mature giant foxtail seeds were collected in the fall of 1999 and 2000 from a nearby location. Empty seeds were removed with an air-column separator, and the remaining seeds were tested for viability using a tetrazolium dye test. Seeds for row-plantings of weeds were buried in the fall in nylon stocking bags to allow after-ripening under field conditions.

All synthetic seedbanks were interred in late October. To place PVC rings in rototilled soil, we stepped on the rim of the rings until the lip protruded about 0.5 to 1 cm above the soil surface. Preweighed seed aliquots were then mixed by hand into the soil to a depth of 5 cm. We chose this depth because giant foxtail germination declines rapidly below a depth of 5 cm (Mester and Buhler 1991). To drive PVC rings into untilled soil, we used a sharp spade to cut a trench around the perimeter of the ring and drove it to within 1 cm of its full depth with a hammer. Giant foxtail seeds were then sprinkled onto surface plant residue to simulate seed dispersal without tillage.

*Seed survival and physiological state.* Two sets of synthetic seedbanks per experimental unit were interred in late October: one was used for determination of percent seed survival from October through March ( $\sigma_{s(w)}$ ), and the other was used for determination of recruitment and seed survival from March through October ( $\sigma_{s(s)}$ ). We did not distinguish between causes of mortality. Before the onset of seed rain, synthetic seedbanks were covered with Agribon® AG-19,<sup>1</sup> a breathable, translucent vegetable row cover, to exclude newly shed seeds.

Two seedbanks per experimental unit in the ST treatment and one seedbank per experimental unit in the FT treatment were excavated in mid-March after the soil had thawed, but no germination had begun. Seedbanks to be used in determining  $\sigma_{s(w)}$  were stored at 5 C until seed extraction. Seedbanks to be used in determining seedling emergence and  $\sigma_{s(s)}$  in the ST treatment were excavated, bagged, and moved to the field margin during spring tillage. Immediately after tillage, these seedbanks were mixed manually to simulate rototilling action and poured back into the PVC rings placed between future corn-row locations. Seedbanks to be used in determining seedling emergence and  $\sigma_{s(s)}$  in the FT treatment were left undisturbed at this time.

Extraction of seeds from synthetic seedbanks was accom-

plished through mechanical washing in an elutriator (Wiles et al. 1996), removing most of the remaining residue with an air column separator and then using a forceps to recover giant foxtail seeds. To test germinability, recovered seeds were incubated for 96 h on moist filter paper at 25 C for 16 h (light) and 15 C for 8 h (dark). Empty or decayed seeds were counted as nonviable. Ungerminated but intact seeds that were classified as viable with a tetrazolium test (Peters 2000) were counted as dormant. Dormant seeds are in a physiological state that impedes germination under environmental conditions that would normally allow germination to occur (Benech-Arnold et al. 2000).

Seed survival from October through March ( $\sigma_{s(w)}$ ) was calculated as  $(N_{MAR}/N_{OCT}) \times 100$ , where  $N_{OCT}$  was the number of viable seeds added to the seedbank in late October in the wheat phase and  $N_{MAR}$  was the number of viable seeds recovered from the seedbank in March in the corn phase. We calculated seed survival from March through October ( $\sigma_{s(s)}$ ) as  $[N'_{OCT}/(N'_{MAR} - N_g)] \times 100$ , where  $N'_{MAR}$  was an estimated value equal to the treatment mean of viable seeds recovered in March from seedbanks used to determine  $\sigma_{s(w)}$ ,  $N_g$  was the total number of seedlings that emerged, and  $N'_{OCT}$  was the number of viable seeds recovered in early October after the corn phase.

*Recruitment.* Corn recruitment was measured as the density of plants within 3 m of row on May 12 and September 9 in 2000 and 2001. Giant foxtail seedling recruitment from synthetic seedbanks was measured weekly from April 27 through June 21 in both 2000 and 2001. Two subsequent censuses indicated that giant foxtail seedling emergence had ceased by June 21. Emerged seedlings were counted and removed using sharp forceps, with minimal soil disturbance, to avoid confounding soil management and emergence-order effects on recruitment. Three indices of emergence were measured for the synthetic seedbanks. Cumulative seedling emergence per square meter was obtained through weekly counts. Emergence as a percentage of viable seeds present in March ( $\gamma$ ) was calculated for each PVC ring as  $(N_g/N'_{MAR}) \times 100$ . Thermal time to 50% seedling emergence ( $T_{50}$ ) was calculated in two steps using nonlinear regression (Weaver et al. 1988). First, a four-parameter Gompertz function was fit to emergence data for each plot:

$$Y = ae^{-be^{-cx}} + d \quad [1]$$

where  $Y$  = cumulative number of emerged seedlings per square meter,  $x$  = growing degree days (base 10 C),  $e$  represents the exponential constant 2.7471, and  $a$ ,  $b$ ,  $c$ , and  $d$  are parameters to be estimated. All curve fits were generated using the least-squares subroutine of Kaleidagraph® v. 3.0.8 (Synergy Software 1998) and inspected for goodness of fit. Equation 1 described the progress of seedling recruitment well, with  $R^2$  values between 0.91 and 0.99. In a second step, Equation 1 was solved for  $x$  when  $Y$  was set equal to 50% of cumulative seedling emergence to give  $T_{50}$ .

### Growth, Survival, and Biomass Production

Giant foxtail seedlings emerging in row-plantings were tagged with toothpicks, and dead seedlings were noted in weekly counts that continued through June 21. Height of giant foxtail and corn plants was measured every 2 wk through late August. Plant survival ( $\sigma_p$ ) was equal to the percentage of giant foxtail seedlings emerged in row-plant-



ings by June 21 that were present as mature plants in late August. Giant foxtail shoot biomass was harvested from row-plantings in early September and oven dried to constant weight before biomass determination.

### *Fecundity*

In early August, before seed rain began, 30 giant foxtail panicles per experimental unit were chosen randomly and enclosed in bags made of Agribon AG-19®.<sup>1</sup> Panicle length was regressed on seed number for bagged panicles in September. We used this method each year to convert measurements of giant foxtail panicle length in the rest of the experimental unit into an estimate of fecundity per plant ( $\phi$ ) and per square meter ( $f$ ) (Forcella et al. 2000). Corn was hand harvested and adjusted to 13% moisture to determine yield.

### *Seed Predation*

Unlike the other demographic parameters in this study, postdispersal predation of giant foxtail seed was measured in the corn, soybean, and wheat sole crops and the wheat-red clover crop mixture. Our rationale for this change in protocol was that seed predators would be more likely to be influenced by the different habitats represented by the different types of crop residue (Carmona and Landis 1999; Carmona et al. 1999) than by changes in soil characteristics associated with different green manure and tillage timing treatments in the wheat phase.

Point estimates of postdispersal seed predation and arthropod seed predator activity-density were obtained using the methods of Menalled et al. (2000). Every 2 wk after onset of seed rain in August 2001, and continuing through early October 2001, 200 viable giant foxtail seeds were placed on a 10- by 10-cm piece of Bemis®<sup>2</sup> humidifier filter that lay flush with the soil surface. As a control treatment, feeding stations were placed in fine wire mesh cages to determine seed losses when predators were excluded. Feeding stations were inspected daily and recovered before all seeds were removed. Daily probability of seed removal was equal to  $C - R^{1/t}$ , where  $C$  and  $R$  were the proportions of viable seeds remaining in the control and uncaged treatments, respectively, when the seed pads were recovered and  $t$  was the number of days the seed pads were left in the field (Mittelbach and Gross 1984).

Arthropod activity-density was measured using pitfall traps. These consisted of 10-cm-diam by 20-cm-tall plastic containers filled to 2-cm depth with a 10% aqueous solution of ethylene glycol. Traps were placed in the field on August 20 to 23 and September 7 to 10, 2001, and were covered between collection dates. Collected insects were frozen until they were identified with help from the Iowa State University Extension Entomology program.

### **Soil Characteristics**

To evaluate the effects of soil amendment and tillage timing on soil properties in the corn phase in 2000 and 2001, each experimental unit was sampled for NO<sub>3</sub>-N, P, K, SOC, and pH (samples collected on June 1) and soil gravimetric water content (samples collected on April 12 and May 10). Fifteen soil cores were taken to a depth of 20 cm in each

experimental unit and bulked to form composite samples. Chemical analyses were performed by the Iowa State University Soil Testing Laboratory using a Cd-reduction assay for NO<sub>3</sub>-N, the Bray-1 method for P, a NH<sub>4</sub>OAc extractant for K, an SMP buffer for pH, and the combustion method for percent SOC (Brown et al. 1998).

Soil amendment and tillage timing effects on soil phytotoxicity during giant foxtail and corn seedling recruitment were assessed with bioassays (Dabney et al. 1996). Forty giant foxtail seeds or 10 corn seeds were spaced in a line 10 cm from the top edge of two 25- by 38-cm sheets of germination paper moistened with 20 ml distilled deionized H<sub>2</sub>O. The field-moist equivalent of 100-g-dry weight soil, collected from each experimental unit on May 10, 2000, and May 17, 2001, was spread in a 1-cm-deep band starting 2 cm above and extending 12 cm below the line of seeds. A third premoistened sheet of germination paper was placed on top of the soil layer, and the entire assembly was rolled along the short axis, wrapped in plastic film, and secured with rubber bands. Units were incubated vertically for 96 h at 25 C in the light (16 h) and 15 C in the dark (8 h). Germinated seedlings were then counted and seedling radicle length measured.

### **Data Analysis**

Cochran's (Underwood 1997) and modified Levene's (Neter et al. 1996) tests were used to assess homogeneity of error variances within and between years. All variables passed both tests, except for  $f$ ,  $\phi$ ,  $\sigma_{s(s)}$ , and  $\sigma_{s(w)}$ , which failed the modified Levene's test across years. A square-root ( $f$  and  $\phi$ ) transformation and an arcsine ( $\sigma_{s(s)}$ ) transformation (Neter et al. 1996) rectified this situation. No transformation worked for  $\sigma_{s(w)}$ , therefore these data were analyzed within years. Raw data are presented in tables for ease of interpretation.

All variables except cumulative giant foxtail emergence per square meter were analyzed with split-plot analysis of variance models that included Year, Tillage timing, and Red clover main effects and interaction terms using the generalized linear models (GLM) subroutine of SYSTAT® 9.0 (Wilkinson 1999). Means were separated by Fisher's Protected LSD test at  $P < 0.05$  (K. A. Gomez and A. A. Gomez 1984). Giant foxtail seedling emergence per square meter was analyzed by repeated measures using the GLM: REPEAT subroutine of SYSTAT® 9.0 (Wilkinson 1999).

A path analysis of the Red clover and Tillage timing effects on  $f$  was performed using methods described by Mitchell (2001). Data were analyzed across years because the component variables in the models, including corn height, giant foxtail biomass, and  $f$ , did not fail tests for homogeneity of error variances, nor were there year by treatment interactions for these variables. Candidate models including manifest and latent variables were compared using the RAMONA subroutine of SYSTAT 9.0 (Wilkinson 1999), and the most parsimonious hypothesis-testing model was chosen based on minimization of Akaike's information criterion (Burnham and Anderson 1998). Path coefficients were computed using the RAMONA subroutine of SYSTAT 9.0 (Wilkinson 1999).

TABLE 1. Giant foxtail seed survival and dormancy measured within a corn crop grown under management treatments varying in tillage timing and crop sequence.<sup>a</sup>

Treatment <sup>b</sup>	Survival				Dormancy			
	October–March ( $\sigma_{s(w)}$ )		March–October ( $\sigma_{s(s)}$ )		March ( $d_w$ )		October ( $d_s$ )	
	2000	2001	2000	2001	2000	2001	2000	2001
	%							
FT/W	91 b	62	50	59	57 a	10 b	40	11
FT/R	86 a	59	56	57	63 b	14 c	37	13
ST/W	87 a	50	54	71	55 a	6 a	34	7
ST/R	85 a	51	56	69	72 c	9 b	31	7
SE	1.1	1.9	1.2	2.5	1.9	1.0	2.2	1.4
Main effect: Tillage timing								
FT	88	60 b	53	58 a	60	12 b	39	12
ST	86	50 a	55	70 b	64	8 a	33	7
Main effect: Red clover								
W	89	56	52	65	56 a	8 a	37	9
R	85	54	56	63	68 b	12 b	34	10

<sup>a</sup> Within columns for each year, means followed by different lowercase letters were different as determined by a Fisher's Protected LSD<sub>0.05</sub> multiple-comparison test.

<sup>b</sup> Treatment abbreviations: FT, fall tillage; ST, spring tillage; W, wheat sole crop before corn phase; R, wheat underseeded with red clover before corn phase.

## Results and Discussion

### Crop Growth and Weed Demography

Interannual variation in most plant growth and demographic variables was greater, by as much as an order of magnitude, than variation due to management effects (Tables 1–4). These data agree with those of Ullrich (2000), who found that weather far outweighed the effects of crop sequence, cultivation, and tillage on weed population dynamics in Maine potato (*Solanum tuberosum* L.)—cropping

systems. However, we did see management effects on plant growth and demography pertinent to our hypotheses.

### Seed Survival and Dormancy

Because of nonconstant error variance across years, seed survival during fall and winter ( $\sigma_{s(w)}$ ) was analyzed within years. A Tillage timing by Red clover interaction ( $P < 0.05$ ) was observed for  $\sigma_{s(w)}$  in 2000 (Table 1). Seed survival was 6% greater in the FT/W treatment (91%) than in all other

TABLE 2. Giant foxtail and corn recruitment within a corn crop grown under management treatments varying in tillage timing and crop sequence.<sup>a</sup>

Treatment <sup>b</sup>	SETFA <sup>c</sup> recruitment				SETFA plant survival ( $\sigma_p$ ) <sup>f</sup>		Corn density (May 12)	
	Cumulative ( $\gamma$ ) <sup>d</sup>		$T_{50}$ <sup>e</sup>		2000	2001	2000	2001
	2000	2001	2000	2001				
	%		GDD <sub>10</sub>		%		10 <sup>3</sup> plants ha <sup>-1</sup>	
FT/W	15 a	33 b	240 a	170 a	91	95	62 b	70 b
FT/R	18 ab	33 b	270 b	170 a	92	94	65 b	73 bc
ST/W	19 b	29 b	240 a	170 a	95	97	44 a	78 c
ST/R	14 a	24 a	280 c	220 b	97	96	41 a	62 a
SE	1.0	1.7	4	5	2	1	3	2
Main effect: Tillage timing								
FT	17	33	260	170 a	91 a	94 a	64 b	72
ST	17	27	260	200 b	96 b	97 b	43 a	70
Main effect: Red clover								
W	17	31	240 a	170 a	93	96	53	74 b
R	16	29	275 b	200 b	95	95	53	68 a

<sup>a</sup> Within columns for each year, means followed by different lowercase letters were different as determined by a Fisher's Protected LSD<sub>0.05</sub> multiple-comparison test.

<sup>b</sup> Treatment abbreviations are defined in Table 1.

<sup>c</sup> Abbreviation: SETFA, giant foxtail.

<sup>d</sup> Seedling recruitment through June 21, when new emergence had ceased, expressed as the percentage of viable seeds in March giving rise to seedlings.

<sup>e</sup>  $T_{50}$  = growing degree days (base 10 C) required to reach 50% emergence.

<sup>f</sup> Seedling survival was expressed as [(number of mature giant foxtail plants in late August)/(number of seedlings that had emerged in row plantings by June 21)]  $\times$  100%.

TABLE 3. Growth and yield of a corn crop under management treatments varying in tillage timing and crop sequence.<sup>a</sup>

Treatment <sup>b</sup>	Corn height				Corn population at harvest		Corn yield	
	June 5		June 22					
	2000	2001	2000	2001	2000	2001	2000	2001
	cm				10 <sup>3</sup> plants ha <sup>-1</sup>		10 <sup>3</sup> kg ha <sup>-1</sup>	
FT/W	63 c	33 c	140 c	70 b	61 b	64 b	15.3	15.3
FT/R	61 c	34 c	140 c	73 b	62 b	65 b	15.3	15.3
ST/W	46 b	29 b	120 b	70 b	49 a	66 b	12.8	13.4
ST/R	42 a	23 a	110 a	60 a	46 a	60 a	12.2	12.8
SE	0.7	1.3	2	1	1.7	0.6	0.6	0.5
Main effect: Tillage timing								
FT	62 b	34 b	140 b	70	62 b	65	15.3 b	15.3 b
ST	44 a	26 a	120 a	65	47 a	63	12.8 a	13.1 a
Main effect: Red clover								
W	55	31	130	70	55	65	14.0	14.4
R	51	29	125	67	54	63	13.8	14.0

<sup>a</sup> Within columns for each year, means followed by different lowercase letters were different as determined by a Fisher's Protected LSD<sub>0.05</sub> multiple-comparison test.

<sup>b</sup> Treatment abbreviations are defined in Table 1.

treatments (86%). This indicates that incorporating fresh red clover residues into the soil may constitute a seed mortality factor comparable with, but not greater than, exposure to the elements, pathogens, and seed predators. In 2001, there was a Tillage timing main effect ( $P < 0.05$ ) on  $\sigma_{s(w)}$ . Seed survival was 17% lower in the ST treatment (50%) than in the FT treatment (60%). Lower values of  $\sigma_{s(w)}$  in the ST than in the FT treatment support the observation that seed mortality factors tend to be strongest at the soil surface (Cousens and Mortimer 1995).

Less variation was observed for seed survival during the growing season ( $\sigma_{s(s)}$ ) than for overwinter seed survival ( $\sigma_{s(w)}$ ). There was a Year by Tillage timing effect ( $P < 0.05$ ) on  $\sigma_{s(s)}$ . Seed survival during the growing season did not differ between tillage treatments (54%) in 2000, but it was 21% greater in the ST treatment (70%) than in the FT

treatment (58%) in 2001 (Table 1). It is unclear why  $\sigma_{s(s)}$  was affected by tillage timing because seeds in both the FT and the ST treatments were distributed evenly throughout the top 5 cm of soil from March through October and, thus, were exposed equally to mortality factors.

A Year by Tillage timing by Red clover interaction was observed for percent dormancy of seeds recovered in March ( $d_w$ ) ( $P < 0.05$ ). In 2000,  $d_w$  was 13 and 29% greater in the FT/R (63%) and ST/R (72%) treatments, respectively, than in the FT/W and ST/W treatments (56%) (Table 1). In 2001,  $d_w$  was 38% greater in the FT treatment (12%) than in the ST treatment (8%) and 38% greater in the R treatment (12%) than in the W treatment (8%). Percent dormancy of seeds recovered in October ( $d_s$ ) did not differ between any of the management treatments in 2000 (36%) or 2001 (9%).

TABLE 4. Giant foxtail growth and fecundity within a corn crop grown under management treatments varying in tillage timing and crop sequence.<sup>a</sup>

Treatment <sup>b</sup>	SETFA height				SETFA biomass		SETFA fecundity			
	June 5		June 22				$\phi^c$		$f$	
	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
	cm				g m <sup>-2</sup>		10 <sup>3</sup> seeds plant <sup>-1</sup>		10 <sup>3</sup> seeds m <sup>-2</sup>	
FT/W	3.5	9.9	16 a	26 a	6 a	190 a	0.1 a	0.9 a	0.5 a	30 a
FT/R	2.8	9.9	21 b	30 b	6 a	210 a	0.2 a	1.1 a	0.6 a	34 a
ST/W	2.4	9.5	25 b	33 b	22 b	300 b	0.6 b	1.3 a	3.4 b	47 b
ST/R	2.2	9.9	23 b	31 b	74 c	460 c	2.4 c	2.0 b	12.1 c	72 c
SE	0.2	0.4	0.8	0.8	8	28	0.2	0.2	1.6	3.7
Main effect: Tillage timing										
FT	2.9	9.9	19 a	28 a	6 a	200 a	0.2 a	1.0 a	0.5 a	32 a
ST	2.5	9.7	24 b	32 b	48 b	380 b	1.5 b	1.6 b	7.8 b	59 b
Main effect: Red clover										
W	3.1	9.7	21	30	14 a	240 a	0.4 a	1.1	1.9 a	38 a
R	2.3	9.9	22	31	40 b	340 b	1.3 b	1.5	6.3 b	53 b

<sup>a</sup> Within columns for each year, means followed by different lowercase letters were different as determined by a Fisher's Protected LSD<sub>0.05</sub> multiple-comparison test.

<sup>b</sup> Treatment abbreviations are defined in Table 1.

<sup>c</sup> The symbols  $\phi$  and  $f$  represent giant foxtail fecundity in seeds per plant and seeds per square meter, respectively.

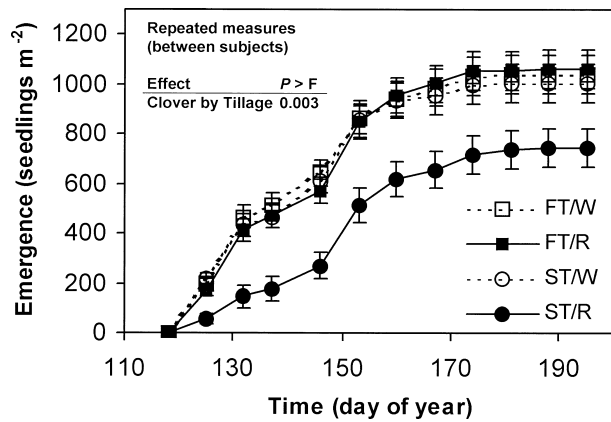


FIGURE 1. Giant foxtail seedling emergence per square meter from synthetic seedbanks under contrasting crop sequence and tillage timing treatments. Treatment abbreviations are defined in Table 1. Data were analyzed over years using repeated-measures analysis of variance. Vertical bars represent  $\pm$  one standard error of the mean of four replicates.

### Seedling Recruitment and Survival

**Corn.** A Year by Tillage timing by Red clover interaction ( $P < 0.05$ ) was observed for corn density both early (Table 2) and late (Table 3) in the growing season. Corn density was reduced in 2000 by 32% in the ST treatment compared with the FT treatment, but it was unaffected by Tillage timing in 2001. Red clover was associated with a 21% reduction in corn density in the ST treatment in 2001, but it did not influence corn density in the FT treatment. Red clover did not affect corn density in 2000.

**Giant foxtail.** Three indices of recruitment from synthetic seedbanks, including total seedlings per square meter, cumulative emergence as a percentage of viable seeds present in March ( $\gamma$ ), and thermal time to 50% emergence ( $T_{50}$ ), showed that seedling emergence in the ST/R treatment was generally reduced and delayed compared with the other treatments. The total number of seedlings emerging per square meter, analyzed across years, was lower in the ST/R treatment than in the other treatments during the entire census period (Figure 1). By the final census date, June 21, 30% fewer seedlings per square meter had emerged in the ST/R treatment (743) than in the FT/R, FT/W, and ST/W treatments (1,034). Results were similar for  $\gamma$ . In 2000 and 2001,  $\gamma$  was 25 and 17% lower, respectively, in the ST/R treatment than in the ST/W treatment, but red clover residues did not significantly affect  $\gamma$  in the fall-tilled treatments (Table 2). Finally, in 2000, red clover residues were associated with 30- and 40-GDD<sub>10</sub> delays in  $T_{50}$  in the FT and ST treatments, respectively (Table 2). In 2001, red clover residues were associated with a 50-GDD<sub>10</sub> delay in  $T_{50}$  in the ST treatment but not in the FT treatment.

Survival of giant foxtail seedlings in row-plantings through reproductive maturity ( $\sigma_p$ ) was 5 and 3% greater in the ST treatment than in the FT treatment in 2000 and 2001, respectively ( $P < 0.05$ ). We speculate that the increase in giant foxtail survival associated with spring tillage may have been due to reduced early corn growth in the ST treatment compared with the FT treatment (Table 3).

### Growth and Fecundity

**Corn.** Both spring tillage and red clover residues were associated with reduced corn height early in the growing

season (Table 3). Tillage timing modified the effect of Red clover on corn height on June 5 and 22 ( $P < 0.05$ ) such that corn height was reduced in the ST/R but not the FT/R treatment. Despite early height reductions, corn yield was unaffected by Red clover (Table 3). Corn yield was 12 and 14% lower in the ST than in the FT treatment in 2000 and 2001, respectively (Table 3).

**Giant foxtail.** Crop and soil management did not influence giant foxtail height on June 5 (Table 4). There was, however, a Tillage timing by Red clover interaction effect ( $P < 0.05$ ) on giant foxtail height on June 22. Foxtail height was greater in the ST than in the FT treatment and greater at the R level than at the W level of the FT treatment (Table 4). There was also a Tillage timing by Red clover interaction on giant foxtail shoot biomass and fecundity ( $P < 0.05$ ). These variables were greater in the ST than in the FT treatment and greater at the R than at the W level of the ST treatment.

We were interested in knowing whether Tillage timing and Red clover effects on giant foxtail biomass and seed production were due to changes in interference from the corn crop or due to the effects of red clover on giant foxtail. These alternate explanations were tested using path analysis, within tillage treatments, of red clover simple effects on corn height on June 5 and on mature giant foxtail biomass and the relationship of these intermediate variables to giant foxtail seed production (Figure 2).

In both the FT and the ST treatments, corn height on June 5 showed a negative association with biomass of mature giant foxtail plants, which in turn showed a positive association with giant foxtail fecundity. However, only one significant link existed between red clover and this pathway: the R treatment was negatively correlated ( $r = -0.24$ ,  $P < 0.05$ ) with early corn height in the ST treatment. The large value of latent variable  $U_1$  indicates that variation in corn height was largely unexplained. Nonetheless, these analyses indicate that reduced interference from corn was the more plausible explanation for increased giant foxtail growth and fecundity in the ST and R treatments compared with the FT and W treatments.

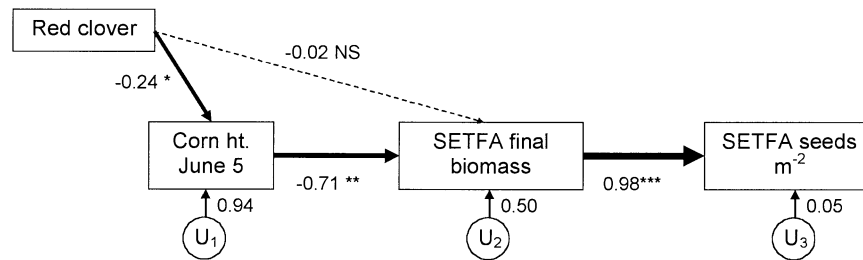
### Postdispersal Seed Predation

Giant foxtail daily seed removal rate in the wheat phase increased from mid-August through late September and then declined through mid-October (Figure 3). At the first four sampling dates in 2001, daily seed removal rate was greater in wheat underseeded with red clover than in the wheat sole crop (Figure 3), after which, seed removal rate was similar for the two crops. The temporal pattern of seed predation was similar for the corn and soybean phases (data not shown). During the period of September 26 to 29, 2001, daily seed removal rate was lowest in soybean (5% of seeds eaten  $d^{-1}$ ), intermediate in corn (18% of seeds eaten  $d^{-1}$ ) and wheat (25% of seeds eaten  $d^{-1}$ ), and greatest in wheat underseeded with red clover (58% of seeds eaten  $d^{-1}$ ).

During the period of September 7 to 10, 2001, activity-density of field crickets (*Gryllus pennsylvanicus* Burmeister) in wheat underseeded with red clover was more than twice that in corn and wheat, but there were no differences in the activity-density of ground beetles (Coleoptera: Carabidae) in the three crops (Figure 4). This indicates that field crickets may have been at least partly responsible for the high rates



## A. Spring tillage



## B. Fall tillage

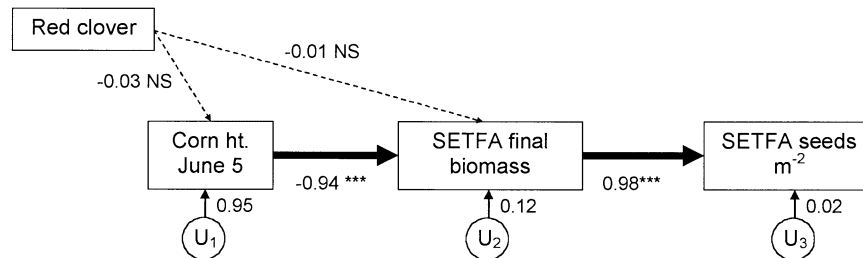


FIGURE 2. Path analysis of red clover effects, within (A) spring and (B) fall tillage treatments, on crop and weed factors related to weed seed production. The relative strength of potential causal pathways is represented by the thickness of the solid arrows, and the symbols \*, \*\*, and \*\*\* represent the significance of path coefficients at the  $P < 0.05$ ,  $0.01$ , and  $0.001$  levels, respectively. Nonsignificant pathways are represented by dashed arrows. Latent variables, or unexplained sources of variation, are represented as  $U_n$ .

of giant foxtail seed predation observed in the wheat–red clover crop mixture compared with the corn and wheat crops. In laboratory feeding studies, adult female and male field crickets ate an average of 26 and 9 giant foxtail seeds per individual, respectively, in a 24-h period (Carmona et al. 1999). The ground beetle species most often found in our pitfall traps, *Harpalus pennsylvanicus* De Geer, is also known to be an important seed predator in agricultural systems (Carmona and Landis 1999).

Differences in habitat quality may have contributed to differences in seed removal rates and insect activity-density. The wheat sole crop and wheat–red clover crop mixture,

which had a twofold difference in predation rates and an eightfold difference in cricket activity-density, also differed greatly in the amount of crop residue present during the study period. After wheat harvest in 2001, modest amounts of wheat stubble (dry weight of  $1.4 \times 10^3 \text{ kg ha}^{-1}$ ), but no living residue, remained in the wheat sole crop, whereas large amounts of live red clover biomass (dry weight of  $[6.0 \pm 0.8] \times 10^3 \text{ kg ha}^{-1}$ ) remained in plots where wheat was underseeded with red clover. Our results corroborate previous studies in which habitat improvement through refuge strips, cover crops, and hedgerows promoted greater post-dispersal seed predation and greater activity-density of arthropod seed predators (Carmona and Landis 1999; Cromar et al. 1999; Menalled et al. 2000).

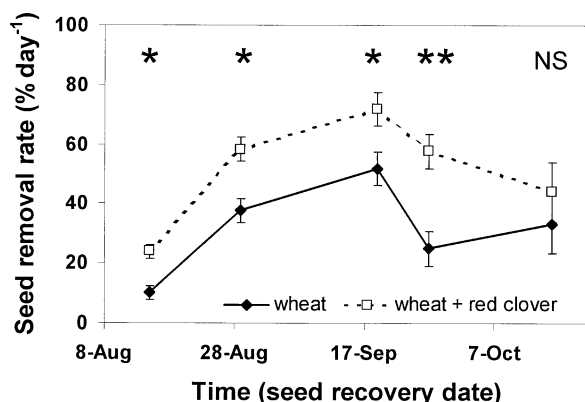


FIGURE 3. Postdispersal predation of giant foxtail seeds at five dates during the period from August 15, 2001, through October 18, 2001, in a wheat sole crop and in wheat underseeded with red clover. Predation rate was expressed as mean percentage of seeds (out of 200) removed per day from feeding stations. Data points are presented at the date of seed recovery. Vertical bars represent  $\pm$  one standard error of the mean of four replicates. The symbols \* and \*\* represent means that are significantly different at the  $P < 0.05$  and  $0.01$  levels, respectively.

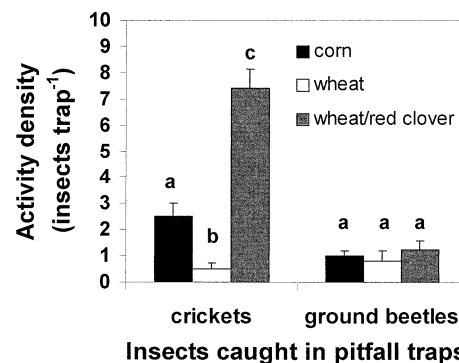


FIGURE 4. Activity-density of field cricket and ground beetles (Coleoptera: Carabidae) in corn and wheat sole crops and a wheat–red clover crop mixture, measured in pitfall traps from September 7 to 10, 2001. Vertical bars represent  $\pm$  one standard error of the mean of four replicates. Within insect groups, means identified by different lower case letters were different as determined by a Fisher's Protected LSD<sub>0.05</sub> multiple comparison test.

TABLE 5. Bioassay of phytotoxic properties of soil collected<sup>a</sup> within a corn crop grown under management treatments varying in tillage timing and crop sequence.<sup>b</sup>

Treatment <sup>c</sup>	Radicle length			Germination		
	SETFA <sup>d</sup>		Corn	SETFA		Corn
	2000	2001	2001	2000	2001	2001
	mm			%		
FT/W	21	20	84	37 b	45 b	99
FT/R	14	13	70	39 b	33 a	100
ST/W	18	19	70	42 b	50 b	100
ST/R	11	12	43	26 a	33 a	100
SE	0.9	1.1	4.8	2.4	2.3	0.2
Main effect: Tillage timing						
FT	17	17	77 b	38	39	99
ST	15	16	56 a	34	41	100
Main effect: Red clover						
W	19 b	20 b	77 b	39 b	47 b	99
R	13 a	13 a	57 a	33 a	33 a	100

<sup>a</sup> Soil was collected on May 10, 2000, and May 17, 2001.

<sup>b</sup> Within columns for each year, means followed by different lowercase letters were different as determined by a Fisher's Protected LSD<sub>0.05</sub> multiple-comparison test.

<sup>c</sup> Treatment abbreviations are defined in Table 1.

<sup>d</sup> Abbreviation: SETFA, giant foxtail.

## Plant–Soil Interactions

Soil amendment and tillage timing effects on soil NO<sub>3</sub>-N and K, the only soil chemical properties affected by management, did not appear to have much influence on giant foxtail demographic parameters in this study. Differences in soil NO<sub>3</sub>-N in the corn phase between the W and R treatments were minor (ranging between 1 and 5 ppm), and in either year, overall soil NO<sub>3</sub>-N levels before urea application were insufficient (ranging between 8 and 15 ppm) to support commercially acceptable corn yields without additional N fertilizer (Voss et al. 1999). Background soil K levels were in the “very high” range (> 110 ppm) for corn production (Voss et al. 1999), and the increase in K levels associated with spring tillage was quite small (3% in 2000 and 8% in 2001).

Soil water and gases have been linked to variation in dormancy and seedling recruitment (Benech-Arnold et al. 2002). Dekker and Hargrove (2002) found that exposure to gaseous O<sub>2</sub> accelerated the after-ripening process of dormant giant foxtail seeds. The effects of Red clover and Tillage timing on the percentage of seeds recovered from synthetic seedbanks in March that were dormant ( $d_w$ ) (Table 1) may have been due in part to differential soil water content during the winter months because  $d_w$  was positively correlated with soil water content before spring tillage ( $r = 0.72$ ,  $P < 0.001$ ). Increased soil water would have decreased the amount of gaseous O<sub>2</sub> in soil pores, thereby decreasing the after-ripening effect of gaseous O<sub>2</sub> on dormant giant foxtail seeds and increasing  $d_w$ , relative to treatments with lower soil water content during winter.

Bioassays showed a consistent inhibitory effect of Red clover on radicle elongation, with 27 and 30% reductions in corn and giant foxtail radicle lengths, respectively (Table 5). There was also a Tillage timing effect on corn, but not on giant foxtail, radicle length, with a 27% reduction in the

ST treatment (56 mm) compared with the FT treatment (77 mm). More recently incorporated plant residues (i.e., those in the ST treatment) were more phytotoxic, as predicted. This result corroborates previous studies of residue-mediated suppression of seedling germination and growth (Breland 1996; Conklin et al. 2002; Dabney et al. 1996). Because residues from both the wheat sole crop and the wheat–red clover crop mixture were present at each factor level for Tillage timing, the Tillage timing main effect indicates that both wheat and red clover residues may have contributed to increased phytotoxicity in the ST treatment. The Tillage timing main effect on corn recruitment and yield appeared to be due to differential phytotoxicity in the ST and FT treatments. Poor seed–soil contact due to clods formed by spring tillage in moist soil may also have contributed to poor corn performance in the ST treatment, but we do not have sufficient data to test this hypothesis.

Main effects of red clover phytotoxicity on giant foxtail radicle elongation were observed in bioassays of soil collected from both the FT and the ST treatments in mid-May. Yet recruitment of giant foxtail was reduced in the ST/R treatment, relative to other treatments, in the field. This discrepancy suggests that other soil properties besides those measured, such as aggregate size and the potential for seed–soil contact, may have contributed to the Tillage timing by Red clover interactions observed in the field.

Identifying mechanisms by which associated changes in soil properties affected seed mortality was beyond the scope of this study. There are many putative abiotic and biotic factors affecting the mortality of seeds in the soil seedbank (Cousens and Mortimer 1995), and there remains much work to be done in determining how agronomic management practices affect ecological determinants of seed mortality.

## Management Implications

The goal of this experiment was to improve understanding of how cropping system characteristics, such as use of green manures and timing of primary tillage, can be manipulated to inhibit weed population growth. One limitation in interpreting the results of this work is that the management treatments had the potential to create large and multiple effects on agroecological interactions among crops, weeds, soil biota, and seed predators that would likely require some time to reach equilibrium. The potential for such interactions highlights the need for long-term studies to fully assess the impact of cropping system diversification and soil management on weed population dynamics. With this caveat in mind, we drew three main conclusions related to cropping system management based on the short-term effects observed in this study.

First, we found that, contrary to Hypothesis 1 (residues of a small-grain–legume green manure will negatively affect all giant foxtail life-stage transitions), tilled residues of wheat underseeded with red clover reduced successful transitions between some giant foxtail life stages in a subsequent corn crop and increased successful transitions between others. The red clover green manure was associated with reduced survival of newly shed giant foxtail seeds and decreased giant foxtail germination, yet there was also a large increase in giant foxtail seed production associated with the ST/R treatment.

Second, we found that tillage timing had both indirect and direct effects on weed demography by regulating the degree of residue-mediated weed suppression and by influencing corn growth and interference against the weed. Green manure appeared to affect demographic processes occurring soon after residue incorporation, supporting Hypothesis 2 (tillage timing should modify residue-mediated weed suppression by a small grain–forage legume green manure). Overwinter survival of giant foxtail seeds was affected by fall-incorporated, but not spring-incorporated, red clover residues. Giant foxtail recruitment was affected by spring-incorporated, but not fall-incorporated, red clover residues. Spring tillage, however, inhibited corn recruitment and early growth, thereby reducing the strength of corn interference against giant foxtail.

Third, we found that levels of interannual variation in giant foxtail demographic parameters greatly exceeded the amount of variation created by the different management practices studied here. Stochastic simulations of weed population dynamics under these and other management scenarios will help determine whether cropping system effects on weed demographic parameters contribute enough to changes in weed population growth rate across growing seasons to constitute important cropping system design factors.

The cropping system characteristics examined in this study were not intended as stand-alone weed management techniques but as a foundation upon which to layer other weed management practices. The next step toward building an integrated weed management system that incorporates the information gained from this study is to identify practices that affect weed demography in ways that are complementary to the demographic effects observed here (Liebman and Gallandt 1997). For example, the seedbank depletion offered by the green manure could be complemented in an LEI system by measures, such as flaming or cultivation, aimed at weed seedling suppression.

Physical and cultural weed control tactics can be used to suppress specific weed life-stage transitions, but there is little information on how such methods, used singly or in combination, affect the entire weed life cycle and the resulting population dynamics. By projecting consequences for weed population dynamics, studies that integrate management effects on weed demographic parameters over the entire weed life cycle will aid the development of more robust strategies for the management of weed populations in LEI farming systems.

## Sources of Materials

<sup>1</sup> Agribon AG-19 floating row cover, PGI Nonwovens, 111 Excellence Way, Mooresville, NC 28115.

<sup>2</sup> Bemis 4035 humidifier filter belt, Bemis Manufacturing Company, 300 Mill Street, P.O. Box 901, Sheboygan Falls, WI 53085-0901.

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