Timing of tillage is an important filter on the assembly of weed communities

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A trait-based community assembly approach to weed management may enhance our understanding of how weed communities respond to specific management practices and increase the utility of weed management based on ecological principles. Therefore, identifying management practices that operate as assembly filters and the species traits upon which they act is an important first step in developing a more predictive weed science. Here, I report results from a 3-yr investigation of the effects of timing of annual tillage (spring vs. fall) on the annual assembly of arable weed communities. The timing of tillage had consistent and dramatic effects on the composition of weed communities; spring tillage led to weed communities dominated by early emerging spring annual forbs and C4 grasses, and fall tillage led to communities dominated by later-emerging forbs and C3 grasses. Traits determining a species' susceptibility to tillage time likely include germination syndrome and life cycle, both of which influence how species respond to changes in soil resource levels and light availability driven by seasonal disturbance regime. Manipulating the timing of tillage and other major soil disturbances may therefore be an important tool for managers interested in influencing community composition or targeting species with similar germination and life-history traits.

Key words: Community assembly theory, disturbance, resource availability, species traits, temporal heterogeneity, tillage, weed ecology.

Determining the extent to which agronomic practices lead to predictable responses in weed community composition and structure is an important and realistic goal of ecologically based weed management (Clements et al. 1994; Smith and Gross 2006). The ability to predict when and how weed communities respond to management practices implies the existence of general principles that can be used to guide weed management decisions and decrease reliance on strategies such as broadcast herbicide applications that have associated nontarget effects (Clements et al. 1994; Maxwell and Luschei 2005). Booth and Swanton (2002) suggest that community assembly theory (Diamond 1975; Keddy 1992; Weiher and Keddy 1999) provides a logical framework to understand how weed community structure changes in response to management practices.

Under a community assembly framework, management practices such as herbicide application, crop rotation, and cultivation are viewed as "filters" that negatively affect the establishment, growth, and reproduction of weed species and therefore reduce the size of the species pool (Booth and Swanton 2002). Weed species that possess traits making them susceptible to a given filter or set of filters are less likely to be present in the weed community following the application of that filter (i.e., they are filtered out). Conversely, weed species that possess traits making them less susceptible to management filtering are more likely to be present in the community. Thus, identifying management practices that act as filters and the traits upon which they act is a first step toward developing greater predictive power regarding which species/traits are likely to become problematic under a given set of management practices (Booth and Swanton 2002; Cardina et al. 2002).

One important filter on weed community assembly is primary tillage (Cardina et al. 2002; Thomas et al. 2004).

Studies documenting increases in later-successional weed species following conversion to no-till indicate that annual tillage tends to favor weed species that complete their life cycle within a year (Derksen et al. 1993). Therefore, viewed under an assembly framework, primary tillage operates as a constraint on community assembly by filtering species with a perennial life cycle, which results in a predictable shift from perennial- to annual-dominated weed communities (Booth and Swanton 2002).

Despite the understanding that tillage itself can be an important filter on weed community assembly, little is known about the degree to which variation in the timing of tillage can further constrain the assembly of weed communities. A number of recent studies have reported differences in the weedy flora between spring- and fall-sown crops (Andersson and Milberg 1998; Hald 1999; Hallgren et al. 1999; Milberg et al. 2001), suggesting that the timing of primary tillage may be an important filter of weed species in annually tilled agroecosystems. But because the identity of crops and associated management practices also vary between spring- and fall-sown cropping systems, it is difficult to separate the effects of these covarying factors from that of tillage time itself. The objectives of the present study were to (1) determine how the timing of annual primary tillage (spring vs. fall), in the absence of other management practices, impacts weed community assembly, and (2) identify associations between the timing of tillage and weed species traits that determine susceptibility to tillage time.

Materials and Methods

Study Site

The study was conducted at the Biodiversity Experiment Plots at the W. K. Kellogg Biological Station Long Term

Ecological Research (LTER) project in agricultural ecology in Hickory Corners, Michigan. Soils at the study site are dominated by Kalamazoo silt loam (Typic Hapludalfs), and are made up of 43% sand, 40% silt, and 17% clay (Robertson et al. 1997). Mean annual temperature at the LTER site is 9.7 C. Annual precipitation is 890 mm[1], with about half in the form of snow (http://lter.kbs.msu.edu/siteDescription.html). Several small-plot studies were conducted in various locations across the site prior to the initiation of the study. These studies, which were conducted over the span of 20 yr, included different annual and perennial crops grown under various management systems; therefore, the composition of the soil seed bank at the initiation of the present study likely included a broad mix of annual and perennial weed species.

The experimental treatments were part of a larger experiment, established in 2000 to examine the effects of cropping system diversity on ecosystem function (Biodiversity Plots Experiment, http://lter.kbs.msu.edu/experimentalDesign.html). For the present study, I compared two treatments that differed in the timing of tillage, but were not planted to crops or amended with any external inputs of fertilizer or pesticide. The tillage treatment consisted of annual spring or fall tillage and subsequent fallow period in which no further cultivation or herbicides were applied. Treatments were replicated across four blocks. The tillage treatments were applied each year, starting in 2000, by chisel plowing and then soil finishing each of four replicate plots (9.1 × 27.4 m) either in the spring (usually mid-May) or fall (late October). The chisel plowing resulted in complete removal and burial of all existing vegetation each year, and finishing leveled the soil. Each year both treatments were mowed in the fall, prior to tillage in the fall-till plots. Tillage and mowing were preformed parallel to the plots to minimize movement of weed seeds between plots.

Vegetation Sampling

Data on the composition and abundance of all species that were present in each treatment were collected each year from 2002 to 2004 (2, 3, and 4 yr after initiation of the treatments). Each August through September, at peak biomass, the identity and number of species within a 1 m² quadrat (species density) was recorded in two central locations in each replicate plot. In addition, all aboveground plant material was harvested from an area of 0.25 × 1 m within each 1 m² quadrat. The location of the 1 m² quadrat was altered each year to avoid sampling in the same place in successive years. Harvested plant biomass was sorted to species, dried to constant biomass at 60 C, and weighed to the nearest 0.01 g. Data from the two subsamples were averaged to obtain a plot-level measure of species density and abundance for each year.

Light and Soil Resource Levels

To determine how resource conditions vary over the course of the season, I measured the light environment and soil resource status in each treatment over the growing season in 2004. Percent active radiation (PAR) reaching the soil surface was measured on three dates (23 July, 22 August, and 19 September 2004) with an AccuPar LP-80 Ceptometer.[1] Soil moisture and total plant-available inorganic nitrogen (NO_3^- and NH_4^+) were measured in fall 2002 and

at three times (28 June, 23 August, and 16 November) in 2004. Soils were sampled to a depth of 25 cm (four 2-cm-diameter cores) in random locations within the central 3 × 9 m of each plot. Aggregated samples were sieved through a 4-mm screen to remove stones and large pieces of organic material. Following sieving, a portion of each aggregated sample (20–30 g) was processed for gravimetric soil moisture analysis. The remaining sample was subdivided; 20 g of each sample was processed for N extraction with 100 ml of 1M KCl (20 g) and the rest air dried and archived. Nitrogen (NO_3^- and NH_4^+) was analyzed with a continuous-flow colorimetric analyzer.[2] Soils were stored at 4 C and were processed within 48 h of collection. Soils sampled in 2002 and on 16 November in 2004 were also analyzed for total mineralizable N following incubation for 28 d at 25 C.

Statistical Analyses

Multivariate analyses were employed to examine differences in community structure between the tillage treatments. Treatment effects on community composition were analyzed with a distance-based multivariate analysis for a linear model (DISTLM v.5, Anderson 2001, 2004). Species abundance data were $\log_{10}(x + 1)$ transformed to increase multivariate normality. For the multivariate linear model, three factors (tillage time, year, and block) were analyzed based on Bray-Curtis dissimilarities with a randomized complete block design with repeated measures. Year was the repeated factor and Block was treated as a random factor. Main effects of timing of tillage (spring vs. fall), year, and their interaction on species abundance was tested with error terms appropriate for a randomized complete block design. The data set was analyzed twice, once with all species, and again with rare species removed. The results were qualitatively similar in both analyses; therefore, results of the analysis, which included all species, are reported here.

Nonmetric multidimensional scaling (NMDS) ordination (McCune and Grace 2002) was used for visual representation of differences in community structure between the tillage treatments. For the NMDS, Bray-Curtis dissimilarity coefficients were calculated on transformed ($\log_{10} x + 1$) species abundance values. Pearson correlation coefficients were calculated between the NMDS ordination axes scores and community-level variables (total biomass, species density, and the Shannon diversity index) to help characterize differences between spring- and fall-tilled weed communities.

Indicator species analysis (ISA, Dufrene and Legendre 1997) was used to investigate individual species response to the tillage treatments, and to determine whether certain species were disproportionately associated with one tillage time over the other. The approach is explained in detail by Thomas et al. (2004). Indicator values (IV) were calculated by multiplying the relative abundance and relative frequency of each species in each treatment across all 3 yr. The IVs can range from 0 (no association with a particular tillage time) to 100 (exclusive association with a particular tillage time). The significance of the indicator value for each species was assessed by a Monte Carlo procedure (1000 permutations) at the $P < 0.05$ level of probability with the use of PC-ORD (McCune and Mefford 1999).

Differences between the two treatments in total com-

FIGURE 1. Photograph of weed communities resulting from spring (left) and fall (right) tillage at the W. K. Kellogg Biological Station Long Term Ecological Research site in Hickory Corners, MI.

munity biomass, species density, the Shannon diversity index from 2002 to 2004, soil resource levels in 2004, and N mineralization in 2002 and 2004 were analyzed with ANOVA under the Mixed procedure (Little et al. 1996) in SAS®.[3] Community biomass and species density data were log and square-root transformed, respectively, prior to analysis, to improve homoscedasticity. Untransformed data are presented in tables and figures.
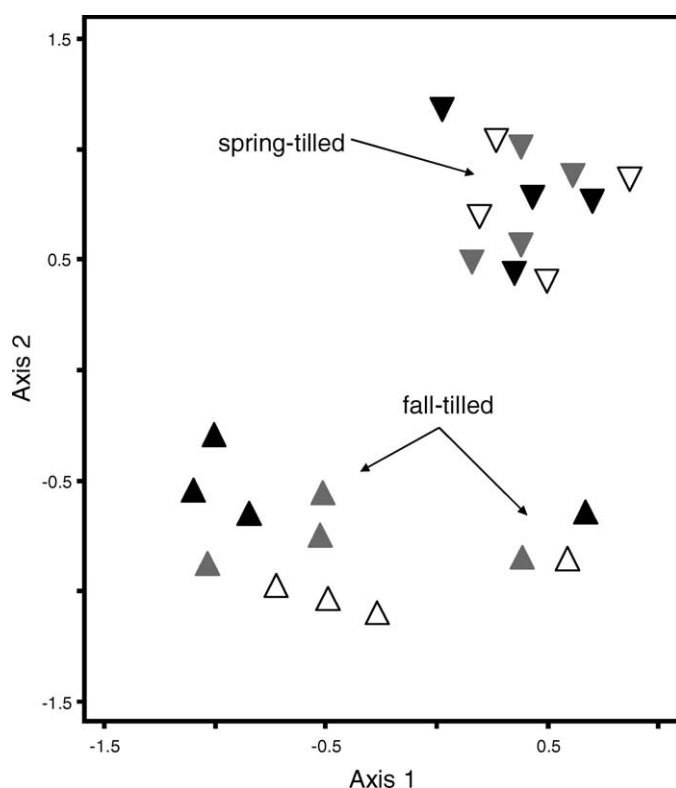

FIGURE 2. Nonmetric multidimensional scaling ordination of plant community abundance data from spring (triangles point down) and fall (triangles point up) tillage treatments at the W. K. Kellogg Biological Station Long Term Ecological Research site in Hickory Corners, MI, in 2002 (black), 2003 (grey) and 2004 (open). Ordination: minimum stress = 8.9, P = 0.02; r^2 = 0.45 (axis 1), 0.47 (axis 2), cumulative r^2 = 0.921.

Results and Discussion

Community Composition and Diversity

In all three years of the study there were visually dramatic effects of the timing of tillage on weed community structure (Figure 1). The distance-based multivariate analysis indicated that timing of tillage, year, and their interaction all significantly affected community composition and abundance (tillage time: pseudo $F_{1,3}$ = 16.5, P < 0.001; year: pseudo $F_{2,12}$ = 4.2, P = 0.006, interaction: pseudo $F_{2,12}$ = 4.0, P = 0.008). The effect of tillage time was evident in the NMDS ordination of the species abundance data, showing a clear and consistent distinction between spring- and fall-tilled weed communities for all three years (Figure 2). The interaction between tillage time and year was also evident in the ordination; fall-tilled replicates tended to cluster by year, whereas spring-tilled replicates had no obvious pattern related to year. The annual community composition of one fall-tilled replicate was somewhat different from that of the other replicates, causing it to cluster away from the other fall-tilled communities in the ordination space.

Correlations between NMDS ordination scores and weed community indices indicated that much of the variation along the ordination axes (particularly the second) was due to differences in species abundance and diversity among replicates, rather than total community biomass (Table 1). In accordance, analysis of variance indicated no difference in total community biomass between the treatments (tillage time: $F_{1,3}$ = 0.18, P = 0.70; year: $F_{2,12}$ = 0.41, P = 0.67;

TABLE 1. Pearson correlations between annual weed community indices and axes scores from a nonmetric multidimensional scaling ordination on species abundance in spring- and fall-tilled treatments at the W. K. Kellogg Biological Station Long Term Ecological Research site in Hickory Corners, MI, from 2002 to 2004.

Weed community indices	Correlation (r)	
	Axis 1	Axis 2
Biomass m^{-2}	−0.184	0.199
Species density m^{-2}	0.130	−0.548
Shannon diversity index	0.054	−0.490

TABLE 2. Annual weed community indices in spring- and fall-tilled treatments at the W. K. Kellogg Biological Station Long Term Ecological Research site in Hickory Corners, MI, from 2002 to 2004.

Tillage time	Year	Biomass[a]	Species density	Shannon diversity index
		(m^{-2})	(m^{-2})	
Spring	2002	562.61 (45.93)	8.88 (0.52)	0.98 (0.10)
	2003	458.92 (62.70)	10.13 (1.38)	0.91 (0.23)
	2004	445.72 (92.43)	10.38 (0.55)	0.75 (0.07)
Fall	2002	411.66 (60.71)	15.75 (2.50)	1.24 (0.31)
	2003	439.60 (26.73)	16.00 (2.61)	1.31 (0.17)
	2004	517.61 (66.85)	15.50 (3.05)	1.26 (0.22)

[a] Values are means ± (SE); $n = 4$.

interaction: $F_{2,12} = 3.69$, P $= 0.056$). Interestingly, despite a trend for higher diversity in the fall-tilled communities (Table 2), and a relatively strong relationship between diversity and the ordination axes, species density and the Shannon diversity index were not significantly different between the spring- and fall-tilled communities when univariate analysis was used (ANOVA, species density: tillage time: $F_{1,3} = 4.48$, P $= 0.12$; year: $F_{2,12} = 0.66$, P $= 0.53$; interaction: $F_{2,12} = 1.15$, P $= 0.34$; Shannon diversity: tillage time: $F_{1,3} = 1.22$, P $= 0.34$; year: $F_{2,12} = 1.57$, P $= 0.24$; interaction: $F_{2,12} = 2.32$, P $= 0.14$).

Species-Specific Responses

A total of 41 species were recorded in the two tillage treatments over the 3 yr of the study. Out of the 41 species, 8 were significantly associated with spring tillage (ISA, P < 0.05), 10 were associated with fall tillage, and the remaining species showed no significant association with either tillage regime (Table 3). Species significantly associated with spring tillage tended to be relatively early germinating forbs such as velvetleaf (*Abutilon theophrasti* Medik.) and lambsquarters (*Chenopodium album* L.), and C4 grasses such as giant foxtail (*Setaria faberi* Herrm.) and large crabgrass (*Digitaria sanguinalis* (L.) Scop.). Species associated with fall tillage tended to be later-germinating forbs such as dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers), mouse-ear cress (*Arabidopsis thaliana* (L.) Heynh.), and horseweed (*Conyza canadensis* (L.) Cronq.), and C3 grass species such as quackgrass (*Elytrigia repens* (L.) Nevski). The strongest tillage time-species association was between fall tillage and the nitrogen-fixing legume red clover (*Trifolium pratense* L.) (indicator value, IV = 90.9), which made up over 35% of the total community biomass in the fall-tilled treatment compared to just 0.4% in the spring-till treatment. Biennial and perennial species appeared to be exclusively associated with fall disturbance (Table 3).

Light and Soil Resource Levels

The timing of tillage contributed to significant temporal variation in soil resource levels and light over the 2004

growing season. At midseason (28 June), soil moisture, inorganic N, and photosynthetically active radiation (PAR) were all higher in the spring-tilled communities compared to the fall-tilled communities (soil moisture: $F_{1,3} = 11.6$, P $= 0.04$; nitrogen: $F_{1,3} = 69.5$, P $= 0.004$; PAR: $F_{1,3} = 23.03$, P $= 0.02$). At late season (23 August), soil moisture was still higher in the spring-disturbed communities (moisture: $F_{1,3} = 13.16$, P $= 0.04$). By the end of the growing season (16 November), levels of soil resources and light were equivalent between spring- and fall-tilled communities (Figure 3).

Timing of Tillage as an Assembly Filter

These results provide compelling evidence that the timing of tillage can be a significant filter on the assembly of weed communities and that key species traits determining susceptibility to tillage-time filtering are germination syndrome (i.e., timing of germination) and life cycle (references in Booth and Swanton 2002). Viewed within the context of community assembly theory, spring tillage acts as a filter on initial community assembly by hindering establishment of later-emerging forbs, winter annuals, C3 grasses and species with biennial and perennial life cycles, whereas fall tillage prevents establishment of early-emerging spring annual forbs and C4 grasses (see Table 3). Others have reported similar differences in the composition of early successional plant communities associated with seasonal variation in the timing of soil disturbance (Crawley 2004; Keever 1950, 1979). Crawley (2004) manipulated the timing of soil plowing (every October, March, or May) for 10 years and found that, in general, fall-germinating species declined under spring plowing, and spring germinators declined under fall plowing.

These results also show that the timing of tillage can impact soil resource availability. This effect is likely both a cause and a consequence of species filtering (Bazzaz 1983; Davis et al. 2000), and helps provide a mechanistic explanation for the somewhat counterintuitive impact of tillage time on early- and late-emerging species. Tillage in the spring eliminates plant biomass at a time when there is typically a flush in soil resources (Chapin 1980). Species that are physiologically adapted to emerge earlier in the growing season are therefore able to take advantage of this flush of resources and have a competitive advantage over species that typically emerge later in the growing season when resources become less available (Davis et al. 2000). Similarly, tillage late in the growing season, when soil nutrients are less abundant—because of uptake earlier in the season and immobilization, removes plant biomass that would otherwise constrain germination and emergence of later-emerging species (Chapin 1980). Later-emerging species, which germinate after fall tillage and over the winter as seedlings, then have a competitive advantage over early-emerging species the following spring.

Despite the striking difference in the functional composition of species in the two treatments, including dominance by nitrogen-fixing legumes in the fall-tillage treatment, there was no indication that species composition differences resulting from tillage-time filtering led to a net change in the availability of soil resources from 2002 to 2004. Net mineralization rates differed between spring- and fall-tilled communities, and appeared to be declining over time in both;

TABLE 3. Yearly abundance and indicator values (IV) of weed species associated with spring and fall tillage treatments at the W. K. Kellogg Biological Station Long Term Ecological Research site in Hickory Corners, MI, from 2002 to 2004.

Species	Traits[a]	Biomass[b]						Indicator species analysis		
		Spring tilled			Fall tilled			Associ-ation[c]	IV	P value
		2002	2003	2004	2002	2003	2004			
		g m^{-2}								
Abutilon theophrasti Medik.	A, forb	13.80	7.70	5.20	0.00	0.00	0.01	S	90.50	0.001
Amaranthus retroflexus L.	A, forb	2.00	0.30	0.03	0.00	0.00	0.00	S	41.70	0.039
Ambrosia artemisiifolia L.	A, forb	3.60	7.40	4.70	27.40	47.80	167.50	F	65.40	0.011
Arabidopsis thaliana (L.) Heynh.	A, forb	0.00	0.00	0.02	6.23	9.93	0.15	F	89.50	0.001
Aster sp.	A, forb	0.00	0.00	0.00	0.00	5.95	0.00	U	16.70	0.492
Barbarea vulgaris Ait. f.	B, forb	0.00	0.00	0.00	0.00	0.49	0.00	U	16.70	0.457
Capsella bursa-pastoris (L.) Medik.	A, forb	0.00	0.00	0.00	0.26	0.93	7.93	U	25.00	0.209
Cerastium fontanum ssp. *vulgare* (Hartman) Greuter & Burdet	B/P, forb	0.00	0.00	0.00	0.00	0.02	1.13	U	16.70	0.476
Chenopodium album L.	A, forb	247.03	72.95	25.97	19.28	12.08	1.21	S	61.20	0.002
Conyza canadensis (L.) Cronq.	A/B, forb	0.00	0.00	0.00	0.57	1.47	3.40	F	75.00	0.002
Daucus carota L.	B, forb	0.00	0.00	0.00	2.11	0.41	32.29	U	25.00	0.198
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	A, C4 grass	4.34	0.99	2.81	3.31	4.12	2.72	U	56.20	0.062
Digitaria sanguinalis (L.) Scop.	A, C4 grass	81.39	42.03	18.03	0.29	0.09	0.02	S	85.90	0.001
Echinochloa crus-galli (L.) Beauv.	A, C4 grass	0.00	0.00	0.34	0.00	0.00	0.00	U	8.30	1.000
Elytrigia repens (L.) Nevski	P, C3 grass	0.09	2.51	1.51	72.91	176.06	130.60	F	59.10	0.015
Eragrostis cilianensis (All.) Vign. ex Janchen	A, C4 grass	0.05	0.02	0.08	0.00	0.00	0.00	S	41.70	0.041
Erigeron sp.	A/B, forb	0.00	0.00	0.00	0.03	1.15	0.00	U	16.70	0.431
Lepidium virginicum L.	A/B/P, forb	0.00	0.00	0.00	0.00	0.00	0.28	U	16.70	0.486
Mollugo verticillata L.	A, forb	0.00	0.06	0.14	0.01	0.00	0.03	U	15.30	0.448
Oxalis stricta L.	P, forb	0.01	0.01	0.01	0.70	0.21	0.03	F	56.80	0.047
Panicum capillare L.	A, C4 grass	0.00	0.00	0.00	0.00	0.01	0.00	U	8.30	1.000
Panicum dichotomiflorum Michx.	A, C4 grass	3.36	0.93	1.21	0.00	0.31	0.08	S	67.80	0.014
Plantago lanceolata L.	A/B/P, forb	0.00	0.00	0.00	0.50	0.76	3.38	U	33.30	0.093
Plantago major L.	P, forb	0.00	0.00	0.00	10.58	1.17	3.55	F	41.70	0.032
Poa sp.	P, C3	0.00	0.00	0.00	0.60	1.16	0.17	F	41.70	0.045
Polygonum aviculare L.	A/P, forb	0.00	0.00	0.00	0.21	2.74	5.58	F	75.00	0.001
Polygonum convolvulus L.	A, forb	0.00	0.00	0.00	0.00	0.01	0.00	U	8.30	1.000
Polygonum persicaria L.	A/P, forb	0.06	0.01	0.00	0.00	0.00	0.50	U	12.20	0.701
Portulaca oleracea L.	A, forb	0.00	0.00	0.00	0.01	0.00	0.00	U	8.30	1.000
Potentilla norvegica L.	A/B/P, forb	0.00	0.00	0.00	0.02	0.02	0.04	U	25.00	0.198
Rumex obtusifolius L.	P, forb	3.00	0.20	2.45	7.63	5.30	0.10	U	32.10	0.527
Setaria faberi Herrm.	A, C4 grass	149.17	209.18	258.67	5.75	0.78	4.78	S	75.00	0.003
Setaria pumila (Poir.) Roemer & J.A. Schultes	A, C4 grass	42.17	109.78	123.82	0.01	3.12	1.83	U	54.70	0.091
Setaria viridis (L.) Beauv.	A, C4 grass	6.25	4.81	0.78	1.70	1.42	0.78	S	66.00	0.009
Silene latifolia Poir.	B/P, forb	0.00	0.00	0.00	1.46	0.00	0.00	U	8.30	1.000
Solanum ptychanthum Dunal	A, forb	0.00	0.00	0.01	0.00	0.00	0.00	U	8.30	1.000
Solidago canadensis L.	P, forb	0.00	0.00	0.00	0.00	19.66	17.72	U	33.30	0.094
Stellaria media (L.) Vill.	A/P, forb	0.00	0.00	0.00	0.57	0.00	0.00	U	25.00	0.225
Taraxacum officinale G.H. Weber ex Wiggers	P, forb	0.00	0.01	0.00	14.95	0.97	0.10	F	81.60	0.001
Trifolium pratense L.	B/P, forb	6.25	0.09	0.02	205.61	137.13	131.68	F	90.90	0.001
Veronica sp.	A, forb	0.00	0.01	0.00	0.00	0.14	0.05	U	15.30	0.493

[a] Life-cycle traits are annual (A), biennial (B), or perennial (P).
[b] Dry weight, mean of four replicate plots.
[c] Associations are spring tillage (S), fall tillage (F), and unassociated with either tillage treatment (U). Species–tillage time associations are based on an indicator species analysis (ISA) performed on species abundance data which were pooled across years (2002–2004). Significance of association was determined at the P < 0.05 level.
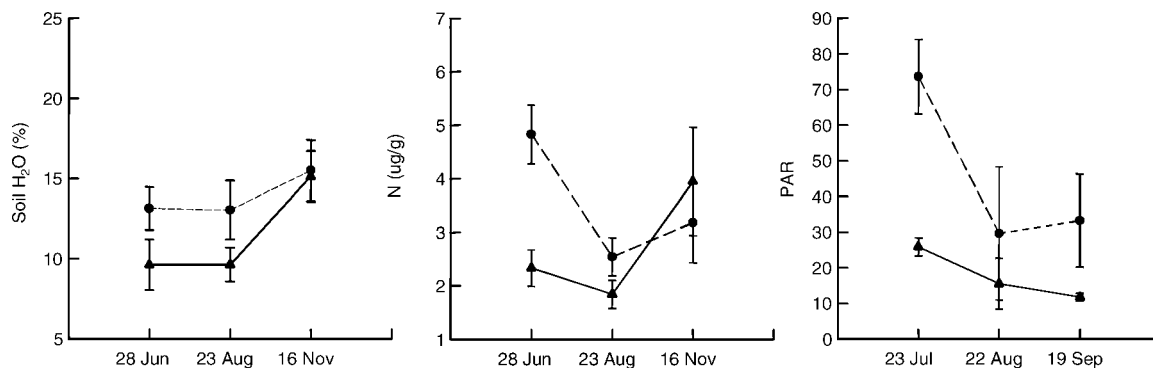
FIGURE 3. Resource levels measured on three dates in 2004 in spring (dashed line) and fall (heavy line) tillage treatments at the W. K. Kellogg Biological Station Long Term Ecological Research site in Hickory Corners, MI. Means ± 1 SE; $n = 4$.

however, the lack of a significant disturbance-by-year interaction indicates that there was no divergence in soil resources between treatments despite the abundance of a nitrogen-fixing legume in the fall-disturbance treatment (Figure 4). This is somewhat surprising, considering the strong effects legumes can have on nutrient cycling in some systems (Mack et al. 2001), and may be due to the relatively short duration of the study. Other species, such as quackgrass, which was also dominant in the fall-tilled communities, may have taken up excess nitrogen provided by the red clover resulting in no net difference in resource levels between tillage treatments.

These results provide support for the hypothesis that variation in weedy floras between spring- and fall-sown crops is due, in part, to differences in the timing of primary tillage (Andersson and Milberg 1998; Hald 1999; Hallgren et al. 1999; Milberg et al. 2001). Interestingly, Milberg et al. (2001) reported that differences in species composition
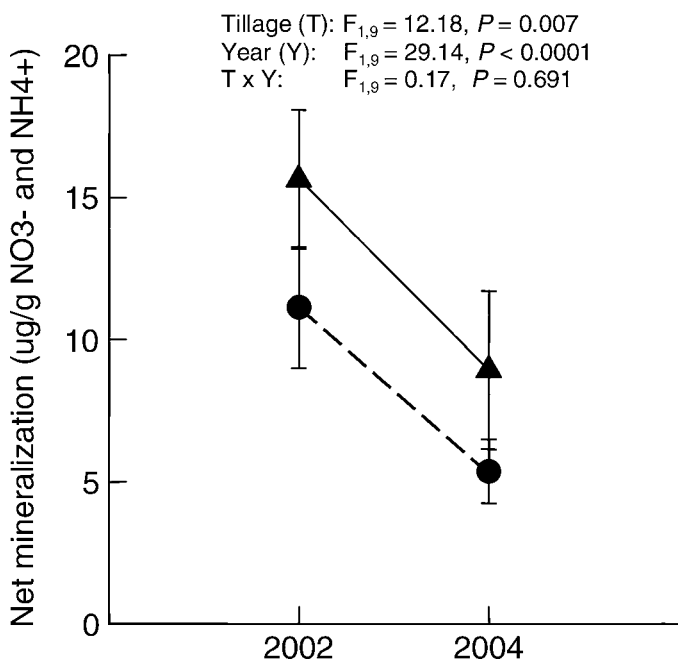

FIGURE 4. Net mineralizable soil nitrogen measured at the end of the growing season (November) in 2002 and 2004 in spring (dashed line) and fall (heavy line) tillage treatments at the W. K. Kellogg Biological Station Long Term Ecological Research site in Hickory Corners, MI. Means ± 1 SE; $n = 4$.

within spring-sown crops were related to variation in the timing of tillage within the spring, suggesting that even smaller-scale variation in the timing of tillage may lead to significant species filtering. Additional studies in which the timing of tillage is varied in weekly intervals will be needed to determine exactly how sensitive a filter interseason tillage time variation is and upon which trait(s) filtering is acting.

Because the goal of this study was to investigate how differences in the timing of tillage drive weed communities along different assembly trajectories, it was necessary to perform the study in the absence of crops and other associated management practices (i.e., fertilizer and herbicide applications). Under more realistic cropping conditions the crop and associated management practices are likely to act as additional filters on weed community assembly (Andersson and Milberg 1998; Booth and Swanton 2002). In conventional systems, for instance, the crop is likely to be the most important filter, as this will determine which herbicides are applied. In an analysis of weed abundance data from multiple tillage studies, Thomas et al. (2004) found few associations between weed species and the intensity of tillage (conventional, reduced, and zero tillage). The authors attributed the lack of observed species association to herbicide applications, which also varied across studies (and were likely stronger filters than tillage intensity), as well as to an absence of basic information on weed species biology and ecology.

However, under alternative management systems, such as organic, other potential filters such as interrow cultivation, cover crops, crop rotation, and seed predation will likely have strong filtering effects on weed communities. Understanding how these factors further constrain the assembly of weed communities, and how they interact with other biotic and abiotic filters, such as insect herbivores, soil pathogens, rainfall, and temperature, should be a fruitful area of research (Belyea and Lancaster 1999; Booth and Swanton 2002; Diaz et al. 1999).

There will be variation among future studies in the specific composition of weed communities that assemble following the application of certain filters. Much of this variation will likely be due to differences in regional and local species pools that determine which species are available for assembly (Andersson and Milberg 1998; Booth and Swanton 2002; Keddy 1992). Although this point may at first seem to negate the predictive power of the community assembly framework, it actually illustrates the utility of a trait-

based approach. Although the abundance and composition of species pools may vary across cropping regions, the traits upon which filters operate likely do not. Therefore, by focusing on the filtering of traits rather than species, predictions are trait specific rather than species specific and are thus likely more generalizable across cropping systems and cropping regions (Booth and Swanton 2002; Thomas et al. 2004).

Conclusions

The present study suggests that disturbance associated with spring tillage will lead to weed communities dominated by early-emerging spring annual forbs and C4 grasses, whereas later-emerging forbs and C3 grass species can be expected to dominate communities under fall tillage. These results have obvious and direct implications for the management of agricultural weeds in annually tilled cropping systems. To increase the predictive power of a community assembly approach, however, the relative importance and interaction of other cropping-system filters such as crop type, fertilizer, and herbicide input will also need to be investigated (Booth and Swanton 2002). In addition, more information regarding the basic biology and ecology of agricultural weeds will be necessary to determine which traits are most likely to confer susceptibility to specific filtering agents (Thomas et al. 2004).

The idea that the timing of disturbance represents an important constraint on community assembly may also have important implications for other managed systems, such as rangelands or areas targeted for restoration or invasive species management aimed at influencing community composition (Emery and Gross 2005; Sheley et al. 2005; Young et al. 2001). For example, manipulating the timing of initial disturbance during restorations in which communities are being reconstructed from a native species pool may lead to very different community outcomes, particularly if the available species differ in traits related to germination and emergence. Additional research will be necessary to determine what additional filters operate in managed ecosystems, their relative strength, and the traits upon which they act.

Sources of Materials

Acknowledgments

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