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Disentangling the Effects of Tillage Timing and Weather on Weed Community Assembly

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Abstract: The effect of tillage timing on weed community assembly was assessed at four locations in the Northeastern United States by tilling the soil every two weeks from April to September and quantifying the emerged weed community six weeks after each tillage event. Variance partitioning analysis was used to test the relative importance of tillage timing and weather on weed community assembly (106 weed species). At a regional scale, site (75.5% of the explained inertia)—and to a lesser extent, timing—of tillage (18.3%), along with weather (18.1%), shaped weed communities. At a local scale, the timing of tillage explained approximately 50% of the weed community variability. The effect of tillage timing, after partitioning out the effect of weather variables, remained significant at all locations. Weather conditions, mainly growing degree days, but also precipitation occurring before tillage, were important factors and could improve our ability to predict the impact of tillage timing on weed community assemblages. Our findings illustrate the role of disturbance timing on weed communities, and can be used to improve the timing of weed control practices and to maximize their efficacy.

Keywords: canonical correspondence analysis; environmental gradient; germination timing; variance partitioning; weed community; weed seed bank

1. Introduction

Understanding factors that influence and structure weed communities in agroecosystems remains one of the most relevant and important goals of community ecologists [1–4]. Emerged weed communities are difficult to predict because almost 90% of potential populations remain dormant in the soil seed bank [5]. Soil weed seed banks can be regarded as the 'memory' of a weed community [6], which is especially true in agroecosystems dominated by annuals. Predicting which species will emerge from the soil weed seed bank and weed community dynamics is challenging because of multiple interactions between abiotic and biotic factors. For instance, seed germination cues, susceptibility to tillage and herbicides, and weed response to crop competition are parameters that vary from one species to another.

Previous research has sought to disentangle the effects of different factors responsible for shaping weed communities, and has examined the effects on weed species richness [4] and weed density [7,8]. Factorial experiments have been performed at the field scale to understand weed community assembly by assessing the effects of management practices including crop rotation [9], tillage [10], and weed control [3,7]. However, Anderson and Milberg [1], using a larger geographical gradient, reported that the greatest differences between weed communities in the sampled regions were due to site characteristics. Beylea and Lancaster [11] proposed a framework for classifying factors that shape weed communities, adapted from Kelt et al. [12], that included: (i) dispersal filters, which determine whether species can disperse to the site, and thus the geographical species pool; (ii) environmental filters, which determine whether species can tolerate the conditions of the site, and thus the habitat species pool; and (iii) internal filters, such as competition, inhibition, and facilitation. Booth and Swanton [13] discuss the application of community assembly theory in weed science and suggest it as a way to overcome the problem of species substitution, which occurs when one problematic weed is effectively controlled but then replaced by a different troublesome weed.

Although the concept of dispersal and environmental filters and the resulting species pools might seem obvious, understanding internal dynamics and how species interact with each other and their environment is complex and one of the greatest challenges in predicting weed communities [13]. For example, Fried et al. [2] found that 89% of the explained variance in weed composition was due to crop type, suggesting that winter, spring and summer-sown cash crops harbor different weed communities with different traits [14]. However, Fried et al. [2] also reported that, after partitioning out the effects of timing of crop sowing and associated tillage practices, and weather conditions, only 18% of the explained variance in weed composition was due to crop type. Tillage is one of the main drivers of weed community assembly because primary tillage concomitantly buries and stimulates the germination of weed seeds [15], and secondary tillage kills the resulting seedlings, thereby decreasing seed density in the soil [16,17].

Weed control practices often drive weed community assembly, as only species that can tolerate or avoid these practices survive and persist in the weed community. One way that weed species can avoid direct control practices is to emerge after they occur. Temperature is an especially critical factor in predicting weed emergence. Soil moisture, related to rainfall patterns, while also important, is a secondary factor only becoming important once the species-specific temperature requirement has been satisfied [18]. Soil moisture and temperature are dynamic parameters linked to daily weather (i.e., ambient temperature, light availability, and rainfall) that affect weed communities [2,4]. However, these abiotic factors can also vary by soil type. Other soil parameters including pH, soil texture [2] and nitrogen [19] are also important for explaining variation in weed composition.

A better understanding of the emergence periodicity of a large number of weed species in relation to the timing of tillage and weather conditions across a large geographical gradient would be valuable. Such information can be used to inform weed management and avoid or reduce the problem of species substitution. Moreover, it can be used to improve weed control efficacy [20,21] and reduce reliance on direct control practices that have a negative impact on the environment such as soil erosion and water pollution [22]. Previous research has demonstrated that the seasonality of tillage (i.e., spring vs. fall tillage) is associated with emerged plant communities that are distinct in species composition [9] and dominant traits [23]. However, few studies have examined the effect of both tillage timing and weather conditions before and after the tillage on weed community assembly. The objective of this research was to quantify the relative importance of tillage timing and weather (temperature and precipitation) on weed community composition, using a variance partitioning statistical approach.

2. Materials and Methods

2.1. Experimental Locations

This multisite experiment was carried out from late April to late September 2013, at four locations across the Northeastern United States (Figure 1). The four sites were (1) Big Flats Plants Material Center in Horseheads, NY, (42.16° N, 76.89° W); (2) Musgrave Research Farm in Aurora, NY, (42.73° N, 76.66° W); (3) Woodman Horticultural Research Farm in Durham, NH, (43.15° N, 70.94° W); and (4) Rogers Farm Forage and Crop Research Facility in Stillwater, ME, (44.93° N, 68.69° W).

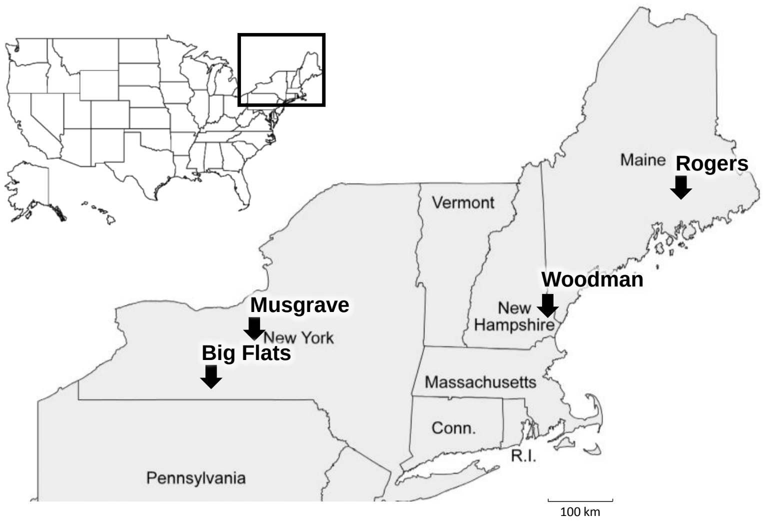

Figure 1. Location of experimental sites in the Northeastern United States.

The four locations have varying soil (Table 1) and climate conditions (Figure 2). The soil texture is dominated by the Unidilla silt loam at Big Flats (coarse-silty, mixed, active, mesic Typic Dystrudepts), the Lima silt loam at Musgrave (fine-loamy, mixed, semiactive, mesic Oxyaquic Hapludalfs), the Charlton fine sandy loam at Woodman (coarse-loamy, mixed, superactive, mesic Typic Dystrudepts), and Lamoine silt loam at Rogers (fine, illitic, nonacid, frigid Aeric Epiaquepts). Musgrave and Big Flats are located in a humid continental climate with warm summer, whereas Woodman and Rogers are located in a humid continental climate with cool summer. The total growing-degree days (GDD with 0 °C base temperature) over the entire experimental period differed between sites (2795 at Big Flats, 2809 at Musgrave, 2859 at Woodman, and 2527 at Rogers).

Tillage was the only treatment applied at all of the sites, except at the Musgrave site, where glyphosate (340 g ae ha^{-1}) was applied at the start of the experiment to suppress crop volunteers. Glyphosate is a systemic foliar-applied herbicide that is assumed to have no soil residual activity, and thus is regarded to have no effect on weeds emerging later in the experiment at the Musgrave site. At all sites, the experiment was established on a homogeneous field (0.25 to 1 ha), previously planted to cereal rye (*Secale cereale* L.) at Big Flats, wheat (*Triticum aestivum* L.) at Musgrave, a mixture of vegetable crops at Woodman, and a green manure mixture of millet (*Panicum miliaceum* L.) and sudangrass (*Sorghum bicolor* (L.) Moench) at Rogers. At the Big Flats site, the field had been used for cereal rye seed production. Prior to producing cereal rye seed, the field was left fallow and mowing was used to control weeds. At the Musgrave site, the field had been managed conventionally for several decades and typically followed a three year corn-soybean-winter wheat rotation. Weeds were managed with appropriate herbicides applied at recommended rates, and in the previous rotation soil was strip-tilled prior to corn and both soybean and winter wheat were no-till planted. At the Woodman site, the field was managed organically for ten years prior to the initiation of the study. During this time, crops included mixed greens grown in low tunnels and rotations of vegetable and cover crops. The field was moldboard plowed each year prior to planting and weeds were managed mechanically with early-season inter-row cultivation. At the Rogers site, the field had been certified organic since 2007 and typically followed a two-year rotation between row crops and spring-planted cover crops. Tillage occurred in the spring and weed management in the row crops was typically achieved with early-season inter-row cultivation, while the cover crops were mowed regularly to limit weed seed production.

2.2. Experimental Treatments

In the Northeastern US, different crops are sown at different times throughout the year, especially vegetable crops. Although previous research has demonstrated that weed communities differ based on the season during which tillage is done (spring vs. fall tillage), we aimed to examine the effect of tillage timing throughout the entire growing season. Thus, we created a gradient of primary tillage events over time. Shallow tillage of treatment plots was performed on a new set of replicate plots every two weeks from 29 April to 30 September, except at the Rogers site where the last treatment occurred on 16 September. The timing of tillage was selected to simulate primary tillage. Treatment plots measured 1.5 by 3.0 m and were replicated four times at all sites, except at the Woodman site, which included five replications. Tillage was carried out using a rototiller (15–20 cm depth) at all sites. Rototillers are considered a primary tillage tool and are commonly used in the region to prepare seedbeds, especially in vegetable production. Tillage treatments were randomly assigned to experimental plots because weeds are known to have a patchy distribution in fields [24]. No crop was grown during the year of the study.

Table 1. Soil pH, organic matter, and macronutrients at each site. †

	Big Flats (NY)	Musgrave (NY)	Woodman (NH)	Rogers (ME)
pH	5.4	7.0	5.2	5.6
Organic matter (%)	2.74	3.58	4.49	4.98
Total Nitrogen (mg kg^{-1})	111.0	188.1	198.8	221.9
Phosphorus (mg kg^{-1})	7.1	5.1	8.0	10.9
Potassium (mg kg^{-1})	49.7	63.5	122.4	129.4
Calcium (mg kg^{-1})	727.7	3348.0	421.0	1167.0
Magnesium (mg kg^{-1})	127.4	317.2	65.61	128.3
Sulfur (mg kg^{-1})	7.3	7.5	17.1	21.1

† A composite soil sample consisting of 12 cores (15 cm depth) was collected from each site at the start of the experiment and analyzed at the Cornell Nutrient Analysis Laboratory. Soil pH was measured using a 1:1 ratio of soil and deionized water, which is then mixed to create soil solution. The pH was determined using an electronic pH meter that measures the electric potential between the soil solution and a reference solution. For macronutrients, the soil was extracted using a modified Mehlich extraction. The extractant solution was then ran on an inductively coupled plasma atomic emission spectrometer. Resulting values are plant available nutrients that is best used as an index of plant availability.

2.3. Plant Sampling

A total of 196 plots were tilled at 12 different timings over the four locations. Plots were sampled for emerged weeds six weeks after the tillage operation. This sampling schedule was used to permit a maximum emergence of weed seedlings while minimizing the potential for competitive exclusion. Weed seedlings in each plot were identified and counted within a randomly placed 0.5 m^2 quadrat within the center of each plot and then converted to the number of plants or stems (for perennials) per m^2. At each site, one person was responsible for weed identification and counting, but multiple researchers provided assistance. Most individuals were identified to the species level and named by their EPPO code (http://eppt.eppo.org/). Some of the plants could only be identified to the genus or family level. Name codes of plants that could not be identified started with 'UNK' (unknown) and were kept in the dataset for calculating weed species richness and total abundance. Crop volunteers (e.g., *Brassica napus* L., *Brassica rapa* L., *Secale cereale* L., *Triticum aestivum* L.) and tree saplings (e.g., *Populus* spp.) were removed from the datasets because their presence in plots was due to the preceding crops and the surrounding landscape (e.g., woodland).

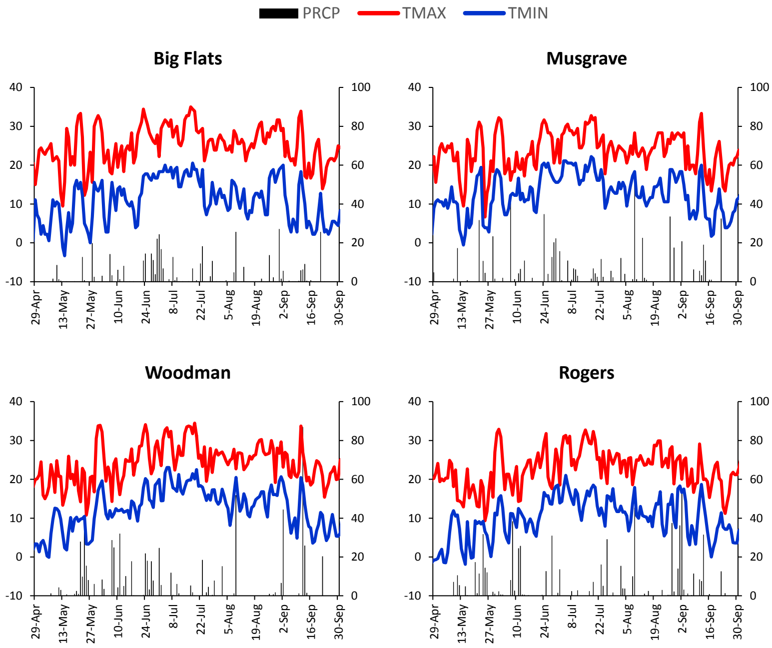

Figure 2. Daily precipitation (PRCP, mm, right *y*-axis, represented by bars), maximum (TMAX) and minimum (TMIN) temperatures (°C, left *y*-axis, represented by lines) from the first (29 April) to the last (30 September) timing of tillage in each of the four locations in 2013. Dates (*x*-axis) correspond to the 12 timings of tillage (except at the Rogers site where the last treatment occurred on 16 September).

2.4. Explanatory Variables

The explanatory variables (Table 2) included three main factors that could account for the assemblage of species in plots: site, weather, and timing of tillage. First, the site was considered a factor accounting for the variability in terms of spatial position (latitude, longitude), soil characteristics (Table 1), past crop and soil management practices, and the regional species pool. Weather data were collected from a weather station located at each experimental site and included rainfall and temperature one week prior and two weeks after the tillage treatment (Table 2). Growing degree days (GDD) were computed using a 0 °C base temperature. Tillage timing was considered a continuous variable (day of the year).

Table 2. Explanatory variables (general meaning and the ranges of values [min–max] by locations) grouped according to the main factors described by them. Data for each tillage date at each site can be found in Table S1.

Explanatory Variables	Meaning	Big Flats (NY)	Musgrave (NY)	Woodman (NH)	Rogers (ME)
PrcpB	Accumulated precipitation (mm) occurring within the week before the tillage	(0–31.4)	(0–51)	(0–115.8)	(0.5–90.5)
PrcpA	Accumulated precipitation (mm) occurring within the two weeks after the tillage	(11.9–101.6)	(19.3–86.8)	(8.6–116.1)	(12.5–94.2)
GDDB	Accumulated growing-degree days (°C) during the week before the tillage	(61.6–176.9)	(56.4–175.3)	(59.7–182.4)	(44.5–162.3)
GDDA	Accumulated growing-degree days (°C) during the two weeks period after the tillage	(166.4–311.9)	(168.3–308.1)	(168.3–316)	(135.8–282.2)
Timing	Date of the tillage (day of the year)	(119 (29 April)–273 (30 September))	(119 (29 April)–273 (30 September))	(119 (29 April)–273 (30 September))	(119 (29 April)–259 (September 16))

2.5. Data Analysis

Pairwise Pearson's correlations between all weather variables and the timing of tillage were performed to check for temporal patterns. The correlation plot was drawn with the corrplot package [25,26]. A detrended correspondence analysis (DCA) was performed with the software Past version 2.17c [27] on the overall plot-by-species (abundance) dataset to observe the ecological gradient length [28], so as to detect any species associations between sites and/or years. DCAs were also performed with the data sets for each site. All DCAs were performed by dividing the first axis into 26 segments. Similarities in weed community between locations were assessed by computing the Sorensen-Dice similarity index for each pair of location. The entire data set (196 plots of 4 sites, 106 weed species described by their aundance, 6 explanatory variables) was then subjected to canonical correspondence analysis (CCA) using 'R' Software [29], as implemented in the Vegan package [30]. All explanatory variables were continuous except the site. We selected species with a frequency of occurrence higher than 5% for the analysis (i.e., occurring more than nine plots), as recommended by Legendre and Legendre [28].

Following the methodology of Lososova et al. [31] and Cordeau et al. [32], both gross and net effects of the 6 explanatory variables (site, PrcpB, PrcpA, GDDB, GDDA, Timing) on weed communities were calculated. Separate CCAs, each with a single explanatory variable (also called constraint), were used to test gross effects. The net effect of each particular variable after partitioning out the effect shared with the other explanatory variables (also called conditionals) was tested with a partial CCA (pCCA), proposed by Rao [33], with a single explanatory variable (i.e., constraint) and the other 5 variables used as covariates (i.e., conditionals). The significance of constraints was tested using permutation based ANOVA (N = 999 permutations). The ratio of a particular eigenvalue to the sum of all eigenvalues (total inertia) was used as a measure of the proportion of variation explained by each explanatory variable [34]. Effects of the groups of variables (e.g., weather) were tested with the same method, that is, with separate CCAs, each for a single group of explanatory variables (gross effect), and pCCAs, each with a single group of explanatory variables (the other groups used as covariates).

3. Results and Discussion

3.1. Weed Communities and Ecological Gradients

For the overall dataset, species richness averaged 6.6 ± 3.1 species m^{-2} and varied by location (ANOVA, F = 31.7, p-value < 0.001). A total of 106 weed species were identified, 35 species at Big Flats (5.2 ± 2.7 species m^{-2} in average), 49 species at Musgrave (7.5 ± 3.4 species m^{-2} in average), 30 species at Woodman (5.0 ± 2.0 species m^{-2} in average), and 38 species at Rogers (9.4 ± 2.0 species m^{-2} in average). Surprisingly, only two species were present at all four sites: *Taraxacum officinale* G.H. Weber ex Wiggers (dandelion) and *Trifolium repens* L. (white clover). Fourteen species were found only at Big Flats, 30 species only at Musgrave, 13 species only at Woodman, and 18 species only at Rogers. Total weed abundance varied from 2 to 1696 plants m^{-2}. Variation in species richness between sites could be due to variation in surrounding landscapes [35] or field edges [36]. However, experiments were conducted away from field edges to avoid this issue, and thus differences in species richness were likely due to differences in cropping history prior to this experiment [1,3,7]. The species richness values at our four sites were comparable to those commonly observed in conventional crop fields [37,38].

Although only two species were present at all four sites, there was overlap in weed communities between sites. Based on the presence-absence of weed species, the Sørensen-Dice similarities between locations were: S(Big Flats/Musgrave) = 0.26; S(Big Flats/Rogers) = 0.33; S(Big Flats/Woodman) = 0.28; S(Musgrave/Rogers) = 0.23; S(Musgrave/Woodman) = 0.23; S(Rogers/Woodman) = 0.35. Relative to large-scale studies, our results are consistent with the literature, where large ecological gradients were observed [2,31,39]. The Sørensen-Dice similarity values suggested that the species pools were partially similar between our four locations. Approximately one quarter to one third of the overall species pool was shared by at least two locations. This is not surprising given the experiments were all conducted in the Northeastern United States during the same year.

Across all sites, the five most frequent species were *Digitaria ischaemum* Schreb. ex Muhl. (smooth crabgrass), *Stellaria media* L. (common chickweed), *Oxalis stricta* L. (yellow wood sorrel), *Taraxacum officinale* G.H. Weber ex Wiggers (dandelion), and *Chenopodium album* L. (common lambsquarters). These species are commonly found in the Northeastern United States [40,41], but also throughout Europe [2] in summer-sown crops [42]. For the entire dataset, 61 of the 106 species recorded had a frequency of occurrence greater than 2% (i.e., more than 4 occurrences) and only 38 species had a frequency of greater than 5% (i.e., more than 10 occurrences). On a site-by-site basis, 18 species at Big Flats, 29 species at Musgrave, 18 species at Woodman, and 21 species at Rogers had a frequency of occurrence higher than 5% (i.e., more than 4 occurrences).

The variability in weed species composition was high between and within locations (Figure 3). The ecological gradient length was 6.4 standard deviation (S.D.) units with the entire data set, 4 S.D. units at Big Flats, 6.2 S.D. units at Musgrave, 4.3 S.D. units at Woodman, and 3.7 S.D. units at Rogers, justifying the use of CCA, which assumes unimodal responses [43,44].

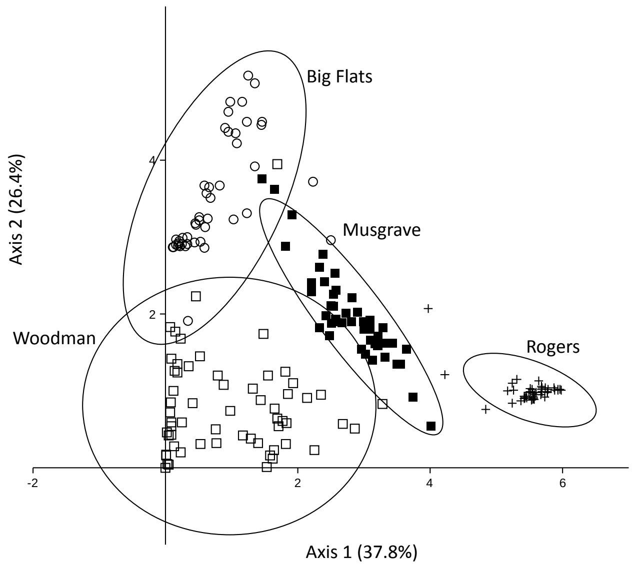

Figure 3. Detrended correspondence analysis (DCA) of the weed communities emerging six weeks after 12 timings of tillage (N = 196 plots) in 2013 in four locations: Big Flats (circle), Musgrave (filled square), Woodman (empty square), and Rogers (cross). Ellipses represent the 95% confidence interval.

3.2. Variability between Locations

We used the results from CCA to examine the gross and net effects of each environmental variable (Figure 4). Across all sites, environmental variables explained 30.6% of the total inertia for the entire dataset (Figure 4, $p < 0.001$). This percentage of explained inertia is consistent with previous weed community studies [2,31,32]. Although this represents a relatively low amount of explanation, which is common in weed community research, it allowed us to evaluate the contribution of individual environmental variables that helped shape the weed community.

The weed community differed between sites (Figure 4), since the gross effect (75.5% of the explained inertia) and net effect (68.5%) of the site were high and highly significant in explaining the weed community variability. The site effect was stronger than, the timing of tillage (18.3%) and the group of weather variables (18.1%) (Figure 4). In previous research, abiotic conditions were identified as key factors shaping weed communities [4]. Grundy and Mead [18] found that meteorological data greatly improved their ability to predict weed emergence. Our results are consistent with these findings because both the gross and net effects of the group of weather variables were significant and accounted for 18.1% and 8.3%, respectively (Figure 4). The net effect of both rainfall variables was low and non-significant, and although the net effect of both temperature variables was also low, the effect for GDD before tillage was highly significant (Figure 4, $p < 0.001$). This suggests that rainfall provided enough soil moisture and that only GDD before tillage shaped the emergence pattern based on the species-specific temperature requirement for germination [18].

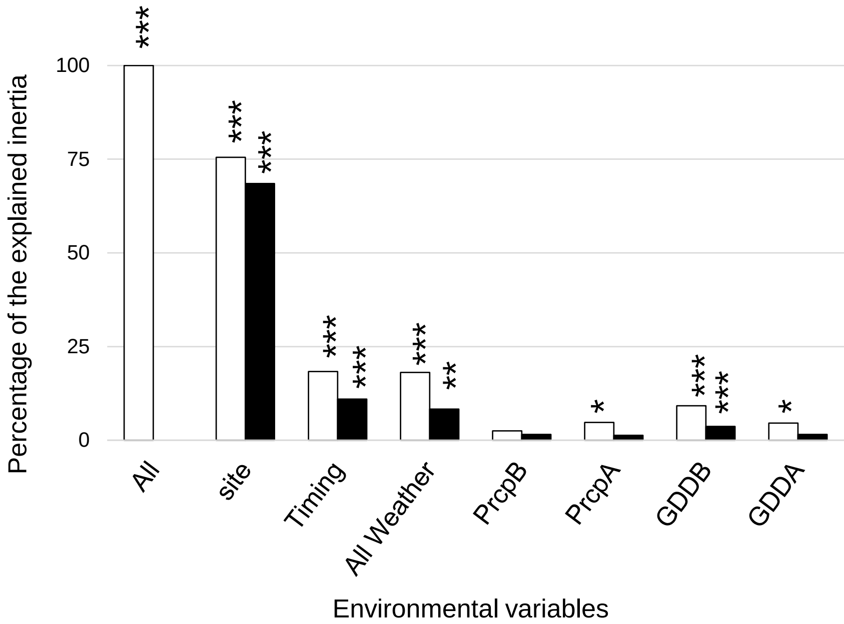

Figure 4. Gross (white bars) and net (black bars) effect of environmental variables on weed community composition of all locations analysed together, obtained with canonical correspondence analysis (CCA) and partial CCA relating the weed community matrix to the environmental matrix. Total inertia explained was 30.6%, represented here as 100%. The significance of constraints was tested using permutation-based ANOVA (N = 999 permutations): * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Weather variables: PrcpB, accumulated precipitation (mm) occurring within the week before the tillage; PrcpA, accumulated precipitation (mm) occurring within the 2 weeks after the tillage; GDDB, accumulated growing-degree days (°C) during the week before the tillage; and GDDA, accumulated growing-degree days (°C) during the two weeks period after the tillage.

The net effect of timing of tillage (10.9%) was significant and similar to the gross effect. This result indicates that the timing of tillage remains highly significant when releasing the effects of the other variables, including the weather and the site. Some species emerged only after the soil was tilled early in the growing season, whereas other species emerged only after the soil was tilled later in the summer. Species emerging early in the season were *D. ischaemum*, *Digitaria sanguinalis* (L.) Scop., *Ambrosia artemisiifolia* L., and *Setaria faberi* F. Herm. (Figure 5). Species emerging only late in the summer were *Thlaspi arvense* L., *Symphyotrichum lateriflorum* (L.) Löve & Löve, *Rumex acetosella* L., Veronica spp., *Cerastium vulgatum* L., and *Veronica peregrina* L. (Figure 5).

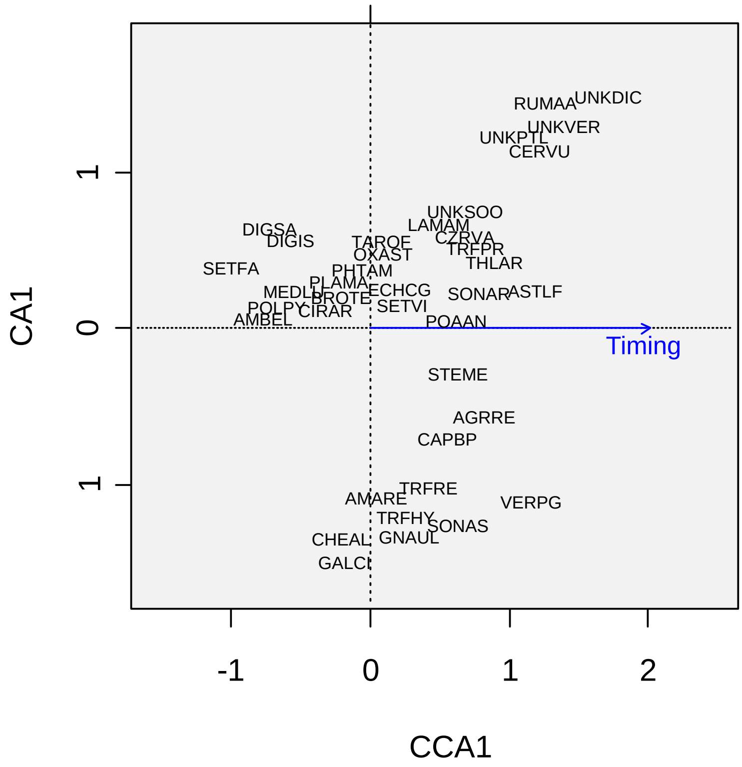

Figure 5. Effect of the timing of tillage (day of the year) on weed community assessed by canonical correspondence analysis (CCA) relating a unique environmental variable (blue) to weed communities (black). Weed species were recorded six weeks after each tillage event, which occurred every two weeks from 29 April to 30 September at the four locations (Big Flats, Musgrave, Woodman, and Rogers). The arrows indicate the direction and magnitude of the response to the timing of tillage. Weed species located in the direction of the arrow emerged later in the summer. Weed species are named by their EPPO code (http://eppt.eppo.org).

3.3. Variability within Locations

At each site, total abundance varied widely with the timing of tillage and tended to decrease over time (Figure 6). No consistent pattern in species richness was observed, but species evenness tended to be lower early in the season and higher later in the season (Figure 6). This result suggests that tillage at earlier dates could be used to promote the emergence of dominant weed species, which can be particularly useful when trying to deplete the weed seed bank using a false seedbed approach [45].

Within each site, CCA were performed with tillage timing and weather variables (Figure 7). At the Big Flats site (Figure 7), Axis 1 explained 65.1% of the variability and separated early tillage (right side) from late tillage (left side). Late tillage events were mainly associated with the emergence of several broadleaf species including *Lamium amplexicaule* L., *Thlaspi arvense* L., *Lotus corniculatus* L., and *Lepidium campestre* (L.) R. Br. Axis 2 explained 18.9% of the variability and was positively correlated with most of the weather variables, largely those describing weather conditions before each tillage event (i.e., PrcpB and GDDB), and to a lesser extent those variables describing weather conditions after each tillage event (i.e., PrcpA and GDDA). Several weed species were strongly associated with high Axis 2 values including *Elytrigia repens* (L.) Desv. ex Nevski, *Trifolium pratense* L., and *Coronilla varia* L. Species like *Echinochloa crus-galli* (L.) P. Beauv. that are commonly observed in summer-sown cash crops such as maize [42,46,47] were associated with high temperatures.

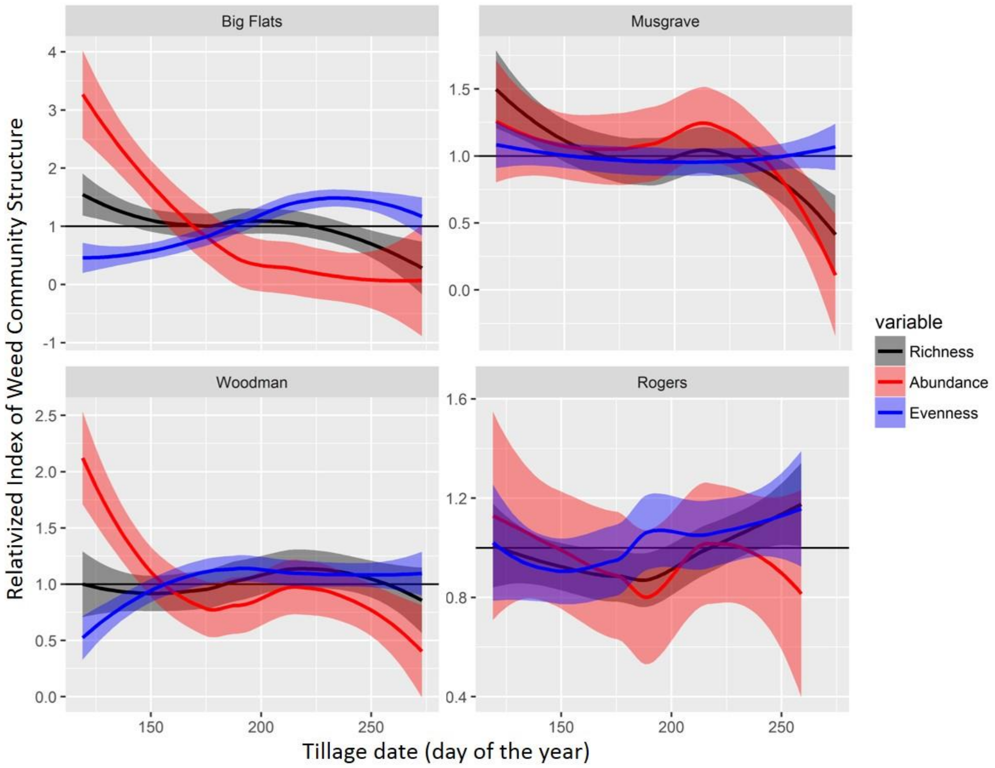

Figure 6. Total weed abundance, weed species richness, and Pielou's evenness over time at the four locations (Big Flats, Musgrave, Woodman, and Rogers). Results are expressed relative to the average (i.e., relativized value = observed value/mean value) of each variable (i.e., total weed abundance, weed species richness, and Pielou's evenness) of weed communities emerging six weeks after tillage (*x*-axis: timing of tillage). Lines represent the smoothed mean and shaded areas represent the 95% confidence interval for each index. For example, at the Big Flats site, weed abundance at the early tillage date was more than three times greater than the average weed abundance from all tillage dates combined.

At the Musgrave site (Figure 7), Axis 1 explained 48.5% of the variability and separated early tillage timings (right) from late timings (left). Species like Chenopodium album were associated with the late tillage timings, whereas species like *A. artemisiifolia*, *S. faberi*, and *Anagallis arvensis* L. were associated with early tillage timings (i.e., late April early May). These results are consistent with known emergence periods for these species [48]. Despite the broad germination temperature range of *Chenopodium album*, a relatively low maximum germination temperature may inhibit its germination during the warmer months of the growing season [49]. Axis 2 explained 20.4% of the variability and was negatively correlated with most of the weather variables and mainly with PrcpB. *Polygonum persicaria* L. and *Setaria viridis* (L.) P. Beauv. were associated with low PrcpB values indicating that tillage could stimulate germination of these species even in dry conditions. The temperature variables (e.g., GDDA, GDDB) were well explained by the combination of Axes 1 and 2, and negatively correlated with early tillage timings.

At the Woodman site (Figure 7), Axis 1 explained 55.6% of the variability and separated early tillage timings (right) from late timings (left). Temperature variables were negatively correlated with Axis 1 and Axis 2, which explained 26.5% of the variability. Fewer species were found early rather than than late. *Trifolium repens* was found late with low GDD, whereas S. media was found late with high GDD.

At the Rogers site (Figure 7), Axis 1 explained 75.2% of the variability and separated the early timings (left) from the late timings (right). Axis 2 explained 13.1% of the variability and was positively correlated with temperature variables. Rainfall after tillage (PrcpA) was positively correlated with

Axis 2 whereas rainfall before tillage (PrcpB) was poorly but negatively correlated with Axis 2. *D. sanguinalis* was associated with early tillage timings. Fried et al. [42] described *D. sanguinalis* as a specialist species of summer crops but mentioned that it could generally grow across a wide range of soil and climatic conditions. *Capsella bursa-pastoris* (L.) Medik. and *Sonchus asper* (L.) Hill. were associated with low GDD.

Tillage timing and weather variables together explained 33.8% of the total inertia at the Big Flats site, 25.2% at the Musgrave site, 33.6% at the Woodman site, and 38.6% at the Rogers site. The importance and significance of these factors in shaping weed communities were tested with CCA and pCCA, and presented as a percentage of the explained inertia (Figure 8). The outcomes were consistent across the site since both the gross and net effects of the timing of tillage and all weather variables considered together were significant (Figure 8). However, both the gross and net effects of all weather variables were stronger than those of the timing of tillage, except at the Rogers site. This result could be due to the Rogers site being the northernmost site (Figure 1) having the lowest GDD (Table 2), which might have affected the relative strength of weather variables compared with the timing of tillage. At most sites, GDD were more significant than precipitation (Figure 8). When precipitation variables were significant, they were representative of conditions before tillage operations (PrcpB) as at the Big Flats and Rogers sites. Precipitation occurring after the tillage (PrcpA) was not significant, except at the Rogers site where this variable had a weak effect. Results from this research should be interpreted with caution since they are from only a single year. However, they are consistent with the literature showing that tillage stimulates germination by moving seeds to the soil surface and exposing them to light [50,51], especially if seeds have adequate moisture [52]. Weed seeds exposed to light when watered germinate better than seeds that are watered in the dark, because light stimulates the release of dormancy in most seeds [52]. Thus, if precipitation occurs before tillage, it could stimulate germination [53], which can be beneficial for depleting the seed bank when using a false seed approach. However, if precipitation occurs and farmers are interested in limiting weed germination, they could dampen germination cues by tilling the soil at night [54].

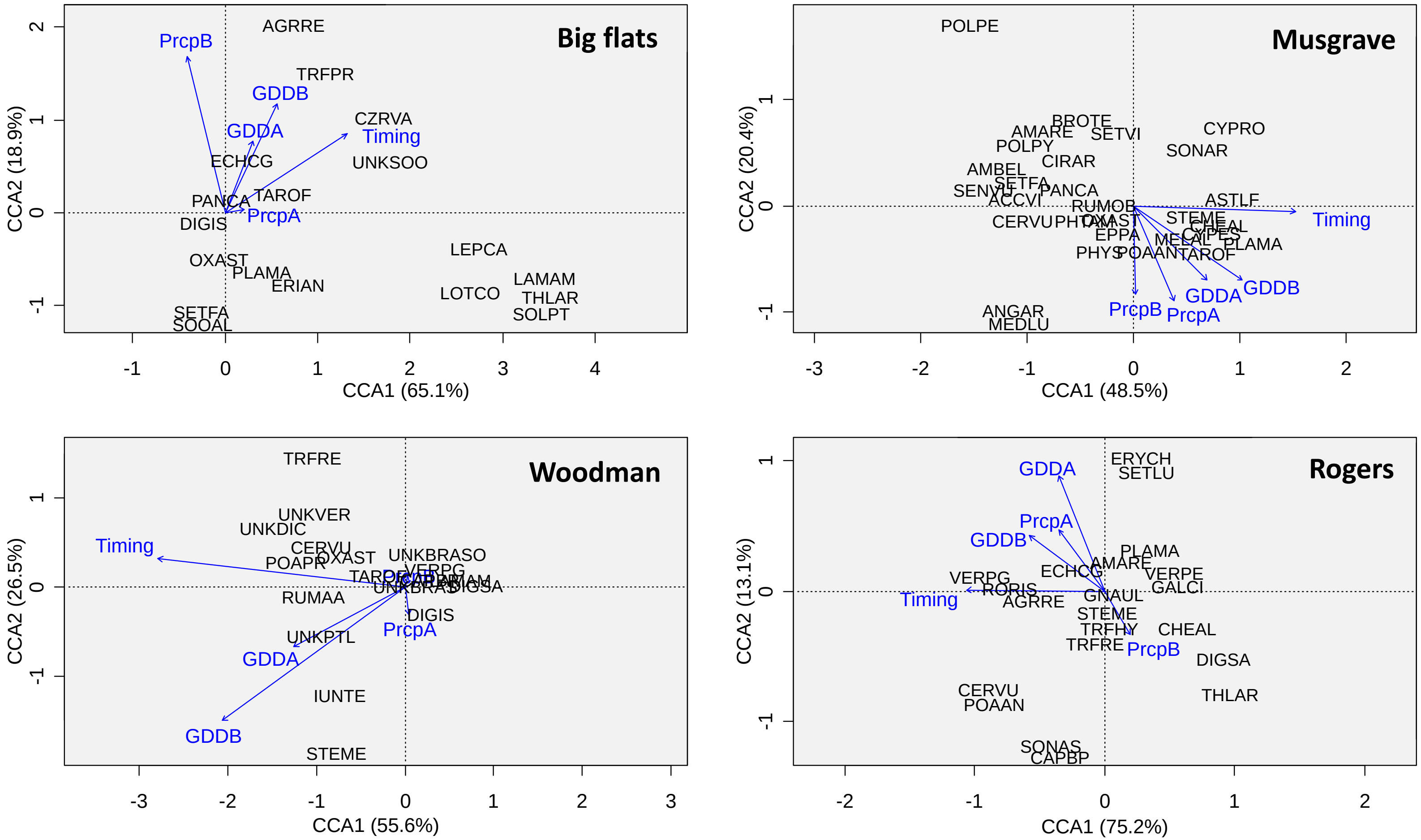

Figure 7. Canonical correspondence analysis (CCA) showing the impacts of environmental variables (blue) on weed communities (black) at the four locations (Big Flats, Musgrave, Woodman, and Rogers). The arrows indicate the direction and magnitude of responses. Weed species are named by their EPPO code (http://eppt.eppo.org). Weather variables: PrcpB, accumulated precipitation (mm) occurring within the week before the tillage; PrcpA, accumulated precipitation (mm) occurring within the two weeks after the tillage; GDDB, accumulated growing-degree days (°C) during the week before the tillage; and GDDA, accumulated growing-degree days (°C) during the two week period after the tillage.

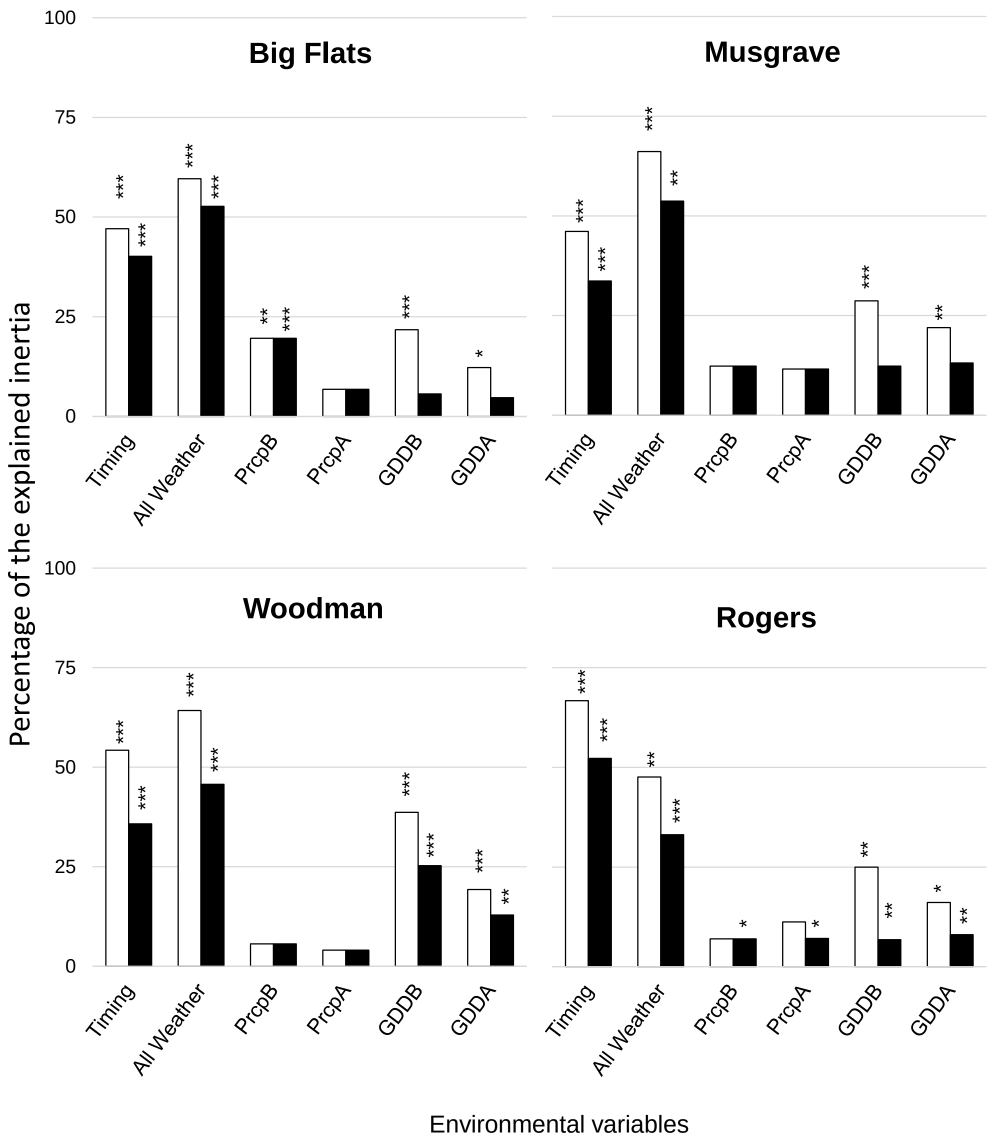

Figure 8. Gross (white bars) and net (black bars) effect of environmental variables (meanings of variables are detailed in Table 2) on weed community composition of locations analyzed separately, obtained with canonical correspondence analysis (CCA) and partial CCA relating the weed community matrix to the environmental matrix. Total inertia explained for each site was 33.8% for Big Flats, 25.2% for Musgrave, 33.6% for Woodman, and 38.6% for Rogers, which was represented here as 100%. The significance of constraints was tested using permutations-based ANOVA (N = 999 permutations): * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Weather variables: PrcpB, accumulated precipitation (mm) occurring within the week before the tillage; PrcpA, accumulated precipitation (mm) occurring within the two weeks after the tillage; GDDB, accumulated growing-degree days (°C) during the week before the tillage; and GDDA, accumulated growing-degree days (°C) during the two week period after the tillage.

3.4. Separating the Effect of Tillage Timing from Weather Conditions

We used correlation analysis to test for temporal patterns with weather variables. A strong correlation would have suggested that effects that we attribute to tillage timing might be explained simply by changing weather. However, no significant correlations were found between the timing of tillage and the other explanatory variables (Figure 9), except a correlation with GDDB (r = 0.45 at Big Flats; r = 0.40 at Woodman; r = 0.64 at Rogers). Thus, it is important to understand both the effect of tillage timing and the effects of weather that occurred before or after tillage events.

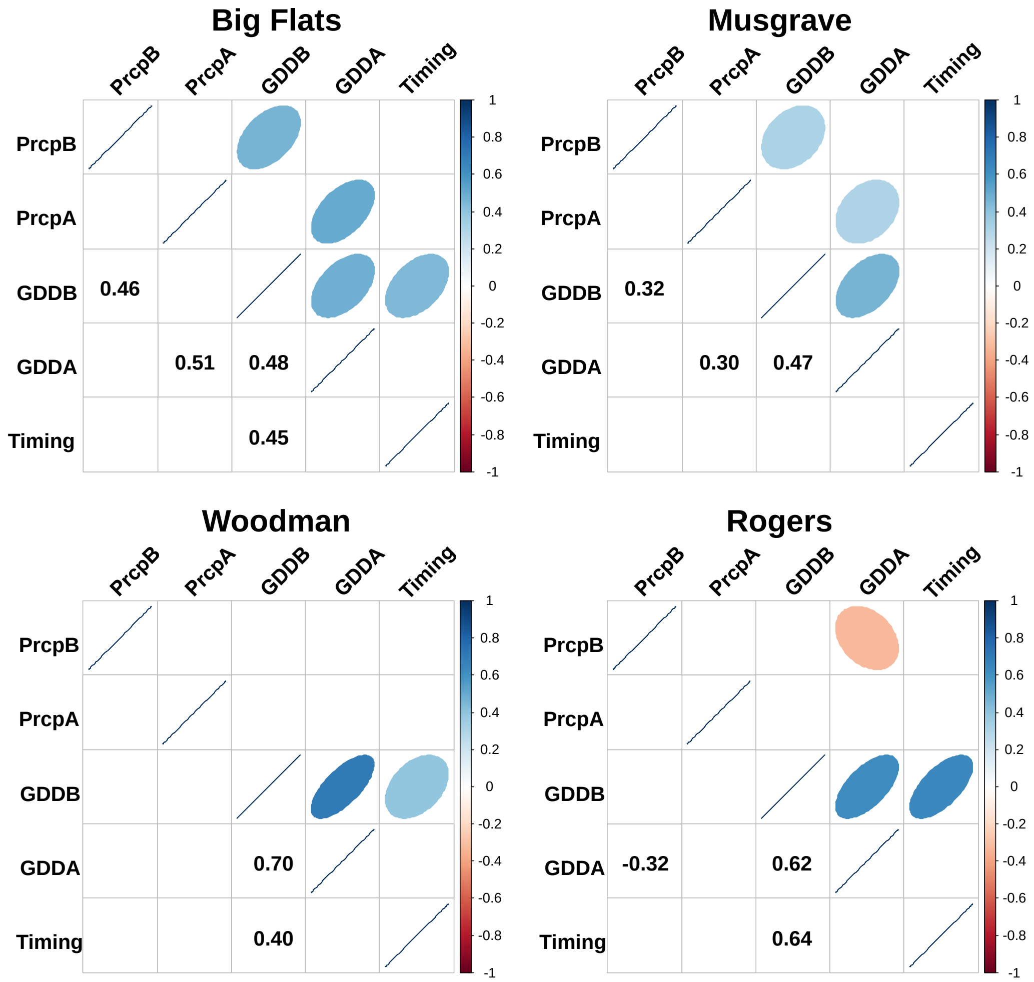

Figure 9. Pairwise Pearson's correlation plot between all weather variables and the timing of tillage. Lower: Pearson's correlation coefficients (*r*). Upper: elliptic representation of Pearson's correlation coefficients (thinner ellipse = stronger link; blue and red = respectively positive and negative correlation). Empty cells are non-significant correlations ($p > 0.05$). Weather variables: PrcpB, accumulated precipitation (mm) occurring within the week before the tillage; PrcpA, accumulated precipitation (mm) occurring within the two weeks after the tillage; GDDB, accumulated growing-degree days (°C) during the week before the tillage; and GDDA, accumulated growing-degree days (°C) during the two week period after the tillage.

We set out to identify which weather variables considered as conditional are likely to decrease the gross effect of the timing of tillage (Table 3). Both the gross effect of tillage timing and its net effect when partitioning out the effect of weather variables were highly significant in all locations (Table 3). The variables GDDB and GDDA, considered as conditional, decreased the gross effect of tillage timing more than other variables. Although both are important, these results suggest that it is more important to consider weather conditions before tillage (GDDB) than after tillage (GDDA) to understand weed community responses to the timing of tillage events.

Table 3. Effect (i.e., percentage of explanation of the total inertia) of timing of tillage (alone and after partitioning out the effects of weather variables) on weed community in the four locations (Big Flats, Musgrave, Woodman, and Rogers).

Model †	Big Flats		Musgrave		Woodman		Rogers	
	Effect	*p* ‡	Effect	*p*	Effect	*p*	Effect	*p*
Y~Timing	15.9	***	11.6	***	18.3	***	25.8	***
Y~Timing + Condition (PrcpB)	15.9	***	11.6	***	18.3	***	25.8	***
Y~Timing + Condition (PrcpA)	15.9	***	11.1	***	18.3	***	24.1	***
Y~Timing + Condition (GDDB)	15.1	***	8.3	***	12.6	***	19.7	***
Y~Timing + Condition (GDDA)	15.9	***	10.4	***	15.4	***	23.6	***
Y~Timing + Condition (all weather variables)	13.6	***	8.5	***	12.1	***	20.2	***

† Models testing the effect of tillage timings (Timing) on the weed community (Y) with CCA and pCCA (for Timing with other variables considered as conditional). Effect values were estimated as the ratio between a particular eigenvalue and the sum of all eigenvalues (i.e., total inertia). When Timing was tested without conditional variables, this corresponds to the gross effect of Timing. When variables are considered as conditional, the effect computed corresponds to the net effect of the Timing when releasing the effect of the conditional variable(s). Weather variables: PrcpB, accumulated precipitation (mm) occurring within the week before the tillage; PrcpA, accumulated precipitation (mm) occurring within the two weeks after the tillage; GDDB, accumulated growing-degree days (°C) during the week before the tillage; and GDDA, accumulated growing-degree days (°C) during the two week period after the tillage; ‡ *p*-Values associated with permutation tests on CCAs and pCCAs: *** $p < 0.001$.

At all locations, when releasing the effect of all weather variables, the net effect of tillage timing decreased (Table 3). This finding supports other studies that have modeled weed emergence based on climatic conditions [18,55,56]. Hydrothermal time has been used previously to improve predictability of the effect of temperature and water availability on seed germination [57–59]. However, the net effects of the timing of tillage remained highly significant ($p < 0.001$) at all locations (13.6% at the Big Flats site, 8.5% at the Musgrave site, 12.1% at the Woodman site, and 20.2% at the Rogers site). This finding suggests that beyond the rainfall and temperature patterns, weed communities remain responsive to the timing of tillage. This outcome suggests that other factors, which were not considered in the analysis, might be responsible for the effects of tillage, within each site. One possible explanation is that precipitation measurements do not adequately reflect soil moisture levels. Indeed, soil moisture can be more accurately modeled with the week-to-week crop moisture index (CMI), which takes mean temperature, total precipitation, and the CMI value from the previous week into account [60,61]. Unfortunately, actual soil moisture data were not collected and thus we cannot provide correlations for the CMI. On the other hand, there might be factors associated with timing that are not represented by the variables we used in the analysis. For example, there could be a progressive increase in plant pests that target seeds and seedlings over the summer [62], or a change in soil nutrient status related to soil processes such as mineralization.

4. Conclusions

Separating the effects of environmental variables from farming practices to explain weed community assemblages at field scales is one of the main challenges in agroecological research. Here, with a multisite experiment across the Northeastern United States, we tested the effects of tillage timing under different weather conditions, soil types, and weed species pools. We demonstrated at a regional scale that site—and to a lesser extent, timing—of tillage, along with weather, shaped weed communities. At a local scale, the timing of tillage explained approximately 50% of the variability. The net effect of tillage timing, when releasing the effect of weather variables, remained significant at all locations. Weather conditions (mainly temperature, but also precipitation) before the various tillage timings should be considered to improve predictions about the impact of tillage timing on weed community assemblages. Ultimately, our findings could be used to improve weed management by adjusting crop rotations, crop planting dates, and the timing of mechanical weed control practices to avoid facilitating the emergence of weed species that are problematic.

Supplementary Materials: The following are available online at http://www.mdpi.com/2077-0472/7/8/66/s1, Table S1: Temperature and precipitation at each location (PrcpB: Accumulated precipitation (mm) occurring within the week before the tillage; PrcpA: Accumulated precipitation (mm) occurring within the 2 weeks after the tillage; GDDB: Accumulated growing-degree days (°C) during the week before the tillage; GDDA: Accumulated growing-degree days (°C) during the two weeks period after the tillage).

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Author Contributions: M.R.R. conceived and designed the experiments; M.R.R., A.T., P.S., R.G.S., E.R.G., and B.B. performed the experiments; S.C. analyzed the data; S.C. wrote the paper; M.R.R., A.T., P.S., R.G.S., E.R.G., and B.B. reviewed the paper.

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