



Intensity of soil disturbance shapes response trait diversity of weed communities: The long-term effects of different tillage systems



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ABSTRACT

Disturbances have a prominent role in structuring plant communities. However, in agroecosystems, the long-term effect of disturbances on determining trait distributions within weed communities remains little studied. We analyzed the effect of three tillage treatments, which differ in the intensity of soil disturbance, on the mean, the range and the distribution of four response traits within weed communities. We aim to test whether tillage acts as a filter restricting the range and the distribution of response traits within weed communities and leads to reduced response trait diversity or whether tilling may have a diversifying effect, creating opportunities for more phenotypes to coexist and increasing response trait diversity. To test this idea, we used data on weed abundance recorded over 24 years from an experiment in which conventional tillage (CT), minimum tillage (MT) and no-tillage (NT) systems were compared. We selected four response traits, maximum height, specific leaf area (SLA), seed weight and seed output, and computed the community weighted mean (CWM) of each trait, as well as four multi-trait metrics related to a different aspect of functional diversity. We found that soil disturbance increases available niche opportunities for weeds especially in terms of regenerative traits. CT, the greater soil disturbance, leads to a greater range and even distribution of the studied traits and that abundant weed species from CT plots hold more divergent trait values than those from MT and NT plots. Our results may be explained by the idiosyncrasy of our disturbance treatments that affect weed seed placement in the soil layers as well as the stratification and availability of soil nutrients. We also found that NT system selected for lower CWM of seed weight (and higher seed output) than MT and CT systems. NT places weed seeds mostly on the soil surface, where having a large seed output may be necessary to avoid the risk of decay or depredation. Conversely, MT and CT systems offer some advantage to other strategies such as larger seed sizes useful to germinate from depth. CWM of SLA was higher in NT and MT than in CT plots and this could be related to greater soil nutrient content in NT systems. In addition our results showed a general trend over experimental time for weed communities to increase in height (and slightly in SLA and seed production) while reducing in seed size. These features are generally associated with intensive farming systems.

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1. Introduction

Species assemble into local communities according to their trait values. Environmental abiotic factors, biotic interactions and stochastic processes act on functional attributes present in the regional species pool to determine the relative abundance of species at local sites (Shipley et al., 2006; Weiher et al., 2011;

Laliberté et al., 2012). The relative importance and the manner in which abiotic factors affect trait distributions within communities are not fully understood. Concerning disturbances, it has been suggested that they may promote a divergent distribution of trait values, thus increasing trait diversity (Grime, 2006). Disturbances may limit the growth and competitive ability of dominant species or promote novel niche opportunities allowing for a variety of phenotypes to occur. Conversely, a high level of disturbance may filter out phenotypes which are unable to cope with the harsh conditions, resulting in a low range of phenotypes and reduced trait diversity (Diaz et al., 1998; Laliberté et al., 2012; Maire et al., 2012). Eventually, the effect of disturbances on trait diversity could depend on the general intensity of disturbance in the

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studied system, on the type of disturbance and on the aspects of functional diversity considered (Bruggisser et al., 2010; Pakeman, 2011).

Agroecosystems are characterized by frequent disturbances, including biomass removal and soil management. Crop type and associated management practices determine the level of disturbance and pose certain limitations on the species found within these systems. Weeds are plant species that accompany crops and that respond distinctly to management practices (Gunton et al., 2011; Fried et al., 2012; Pinke et al., 2012). Weeds are recognized to hold a key role within agroecosystems; they are the greatest contributor to plant diversity, they represent crucial resources for other taxa and they may provide crops with important ecosystem services (Marshall et al., 2003; Moonen and Bàrberi, 2008; Petit et al., 2011). Nevertheless, when occurring in large abundance, weeds are also responsible for reductions in crop yields. The goal is to facilitate a balanced trade-off between the preservation of weed diversity and the maintenance of crop production. Traditionally, weed studies have concentrated on only one or a few dominant species (e.g., Oveisi et al., 2013) but assessing how management practices affect trait distributions within entire weed communities may be an opportunity for developing community-oriented weed management strategies (Storkey et al., 2010; Gunton et al., 2011; Fried et al., 2012). In this context it is useful to refer to the response-effect framework (Lavorel and Garnier, 2002; Suding et al., 2008), and focus on response traits, i.e., those that determine the way communities respond to environmental drivers.

This work analyzes the effect of tillage intensity on both the mean value of response traits in weed communities and on the range and distribution of response trait values within these communities, i.e., weed response trait diversity. Tillage intensity was used as a surrogate for soil disturbance. Three tillage treatments were compared: conventional tillage (CT; plough plus cultivator), minimum tillage (MT; chisel plus cultivator) and no tillage (NT). Tillage is commonly used as a weed management practice to remove the first emerged cohorts of weeds prior to sowing. Tillage can be performed with different implements leading to more or less soil disturbance (CT vs. MT). A similar elimination of weeds can be accomplished by applying herbicide without tilling the soil (NT). Tillage affects the structure and properties of soil as well as the distribution of weed seeds in the soil layers (Swanton et al., 2000; Spokas et al., 2007; Vogeler et al., 2009). Thus, tillage has a potential impact on weed establishment and the distribution and availability of nutrients to weeds.

Specifically, the aims of this research were to test whether (1) tillage acts as a strong filter restricting the range of weed phenotypes which can persist in a field. Greater tillage intensity would therefore result in reduced response trait diversity of weed communities. Or (2) whether tillage opens up available niche space, thus promoting wider ranges of phenotypes. In this case, greater tillage intensity would result in increased response trait diversity of weed communities.

In order to test these hypotheses, weed abundance data recorded during 24 years from a long-term experiment in which a cereal-legume rotation was subjected to the three tillage systems (CT, MT and NT) was used. We selected four response traits, which have been previously related to the response of plants to disturbance and competition, two related to the established phase of plants' life cycle and two associated with the plants' persistence. We used four metrics to characterize weed trait diversity, each related to a different facet: richness (FRic), evenness (FEve), divergence (FDiv) and dispersion (FDIs). We also computed the community weighted mean (CWM) of each of the response traits considered.

2. Methods

2.1. Study site and experimental design

The study was conducted at El Encín Experimental Station (40°29'N; 3°22'W, Madrid, Spain, 610 m.s.l.). The experiment was initiated in 1985 and is ongoing. This paper refers to weed surveys conducted from 1985 to 2011 (24 years of data, no data for 1990 and 1997). The site has a Mediterranean climate, with mild, humid winters and dry, hot summers. Average annual rainfall during the 26-year study period was 445 mm (ranging from 264 to 759 mm). Average annual temperature was 13.8 °C (ranging from 11.9 to 15.5 °C). The soil of the experimental field is an alfisol xeralf, from the calcicortico-molic subgroup.

The experiment followed a randomized block design with four replicates. The three tillage treatments, CT, MT and NT, were randomly assigned to plots (20 m × 40 m) within each block. The cropping system was a rotation of winter wheat (*Triticum aestivum* L.) and a leguminous crop, vetch (*Vicia sativa* L.) or pea (*Pisum sativum* L.). The wheat planting date ranged from October 30th to December 19th. Fertilizers were applied at planting time (28 kg N, 37 kg P₂O₅, 26 kg K₂O ha⁻¹; average rates) and at mid-tillering (53 kg N ha⁻¹), and post-emergence herbicide (0.2 kg a.i. ha⁻¹ ioxynil + 0.2 kg a.i. ha⁻¹ bromoxynil + 1.012 kg a.i. ha⁻¹ mecoprop) was applied at the tillering stage. Leguminous crops were in all cases planted between November 6th and January 19th. Fertilizers were only applied at planting time. Average rates of fertilizer were 14 kg N, 14 kg P₂O₅ and 14 kg K₂O ha⁻¹ for vetch and 19 kg N, 38 kg P₂O₅ and 71 kg K₂O ha⁻¹ for pea. No post-emergence herbicides were applied. CT involved at least one mouldboard ploughing operation with a working depth of 25 cm, followed by a secondary tillage operation with a field cultivator (10–15 cm working depth). MT involved a primary cultivation with either a chisel plow (15–20 cm working depth) or a field cultivator, followed by a secondary operation with a field cultivator. In NT, the only operation conducted prior to wheat planting was the application of glyphosate® (0.72 kg a.i. ha⁻¹) 4–6 days prior to planting. When sowing leguminous crops with NT treatment, straw and stubble from the previous wheat crop were destroyed by chopping, applying non-selective herbicide (e.g., glyphosate) thereafter.

2.2. Weed sampling

Weed species abundance was recorded yearly (except in 1990 and 1997) in ten samples (30 cm × 33 cm per plot), except the first three years when only five samples were collected and in 1995 when 20 samples were obtained. Samples were located along an M-shaped itinerary at intervals of approximately 15 m and 3 m away from field borders. Sampling always took place before herbicide application, between mid February and mid April every year. Sampling time was decided according to crop maturation stage, corresponding to mid-tillering for wheat and stem elongation for vetch and pea.

2.3. Weed response trait data

We chose two response traits related to plants' vegetative phase, specific leaf area (SLA) and maximum height, and two more related to the regeneration of plant species, seed weight and fecundity. SLA is a component of the leaf economic spectrum (Wright et al., 2004). It expresses the potential area available for light interception per unit of dry leaf mass and reflects a trade-off between construction cost, water loss through transpiration and carbon gain through high photosynthetic rates (Westoby, 1998). Plant height is a whole plant trait that, in herbaceous plants, is often related to overall plant size and competitive interactions for

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