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# Tillage as a driver of change in weed communities: a functional perspective

L. Armengot[a,b,1], J.M. Blanco-Moreno[a,1], P. Bàrberi[c], G. Bocci[c], S. Carlesi[c], R. Aendekerk[d], A. Berner[b], F. Celette[e], M. Grosse[f], H. Huiting[g], A. Kranzler[h], A. Luik[i], P. Mäder[b], J. Peigné[e], E. Stoll[d], P. Delfosse[k], W. Sukkel[g], A. Surböck[h], S. Westaway[j], F.X. Sans[a,*]

[a] Agroecosystems Research Group, IRBio, University of Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain
[b] Research Institute of Organic Agriculture (FiBL), Ackerstrasse 113, CH-5070 Frick, Switzerland
[c] Institute of Life Sciences, Scuola Superiore Sant'Anna, Piazza Martiri della Libertà 33, 56127 Pisa, Italy
[d] Institut fir biologësch Landwirtschaft an Agrarkultur asbl IBLA Luxembourg, 13, rue Gabriel Lippmann L-5365 Munsbach, Luxembourg
[e] ISARA Lyon, 23 rue Jean Baldassini, 69364 Lyon cedex 7, France
[f] University of Kassel, Faculty of Organic Agricultural Sciences, Department of Organic Farming and Cropping, Nordbahnhofstr. 1a, 37213 Witzenhausen, Germany
[g] Wageningen University and Research Centre, Applies Plant Research, Edelhertweg 1, 8219 PH Lelystad, The Netherlands
[h] Research Institute of Organic Agriculture (FiBL) Austria, Doblhoffgasse 7/10, A-1010 Wien, Austria
[i] Estonian University of Life Sciences (EULS), Kreutzwaldi 1, 51 014 Tartu, Estonia
[j] The Organic Research Centre, Elm Farm, Hamstead Marshall, Newbury, Berkshire RG20 0HR, United Kingdom
[k] Luxembourg Institute of Science and Technology, 41 rue du Brill, L-4422 Belvaux, Luxembourg

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ABSTRACT

The adoption of non-inversion tillage practices has been widely promoted due to their potential benefits in reducing energy consumption and greenhouse emissions as well as improving soil fertility. However, the lack of soil inversion usually increases weed infestations and changes the composition of the weed community. Weed management is still a main drawback for the wider adoption of reduced tillage practices. However, it is not entirely clear whether these changes in weed communities are a consequence of non-random filters on the functional attributes of weed species and may thus affect the potential weed-crop competition relationship.

Here, we analyse the changes in weed diversity, community composition, and the functional attributes of weed communities under reduced (non-inversion) and conventional (inversion) tillage. We discuss their potential effects on the competitiveness against crop production using data from two crops of seven on-going organic and low-input field trials in different climatic regions across Europe. Weeds were evaluated after post-emergence weed control methods. We used the community weighted mean values of the life form (annuals versus perennials), specific leaf area, seed weight, canopy height, seed bank longevity, soil nutrient conditions affinity, beginning of flowering and flowering span. Moreover, the effect of the crop type on the functional attributes was also evaluated.

Overall, the tillage system affected the composition and functional attributes of the weed communities. Weed community changes may imply a reduction in weed-crop competition under both tillage systems. For instance, weed communities under reduced tillage were potentially less competitive because they were shorter and had less affinity to nutrients. On the other hand, weed communities under conventional tillage had potentially less seed production and a lower abundance of perennial species. Our study thus supports tillage as an important driver of the functional attributes of weed communities, but both tillage systems can have their downside. However, the crop type was overall more relevant than the tillage in determining most of the trait values of the weed communities.



## 1. Introduction

The adoption of reduced tillage practices, e.g., non-inversion tillage, has increased worldwide in recent years (Kassam et al.,

* Corresponding author at: Plant Biology Department, University of Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain.
*E-mail address:* fsans@ub.edu (F.X. Sans).
[1] These authors contributed equally to this publication.

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2010). Reduced tillage has been promoted by international institutions such as the Food and Agriculture Organization of the United Nations and the Common Agricultural Policy in the European Union due to their potential benefits in improving soil fertility, increasing biodiversity, and reducing soil erosion, energy consumption and the emissions of greenhouse gases (Basch et al., 2011; Berner et al., 2008; Hobbs et al., 2008; Holland, 2004).

One of the main concerns of farmers in adopting reduced tillage practices is weed infestation. Tillage is considered to be a key strategy for weed control, particularly under organic farming, where the use of herbicides is prohibited. The lack of soil inversion may increase weed infestation, although this trend is usually crop-specific and not constant over time (Armengot et al., 2015; Légère et al., 2013; Vakali et al., 2011). However, a higher weed infestation under reduced tillage does not always lead to increased yield losses compared to conventional tillage because weed abundance may not reach the level for significant yield loss reduction (Armengot et al., 2015; Sans et al., 2011).

Studying weed communities under both conventional and reduced tillage systems is crucial for overcoming what is perceived as one of the main drawbacks of reduced tillage by farmers. Until now, most studies have focused on the role of the tillage system on weed abundance, community composition, and diversity. The reduction in the intensity of the soil tillage commonly increases the abundance of perennial and grass species (Armengot et al., 2015; Melander et al., 2013; Peigné et al., 2007; Santín-Montanyá et al., 2013), but the trends are less clear in relation to weed diversity (Armengot et al., 2015; Hernandez Plaza et al., 2011; Santín-Montanyá et al., 2013). However, in spite of the evidence that the tillage system may differently affect each species in relation to its attributes such as life form (annual and perennials), trait-based approaches have been neglected in disentangling the effect of reduced and conventional tillage practices on the weed flora (but see Fried et al., 2012; Trichard et al., 2013).

In contrast to the taxonomic approach, the functional attributes of the species allow for the interpretation of shifts in community composition beyond the changes that may be related to the geographic context or to the high variability in the local occurrence of weeds (Gunton et al., 2011). Shifts in weed communities result from non-random filters acting on the local pool of species depending on their functional attributes (Garnier and Navas, 2012; Shipley et al., 2006). Thus, researchers have recently focused their efforts on identifying which farming practices are the most significant filters for weed community assemblies (Gaba et al., 2014; Fried et al., 2012; Trichard et al., 2013). Among others, crop type, fertiliser and herbicide inputs have been found to have a strong influence on weed communities (Fried et al., 2012; Gunton et al., 2011; Storkey et al., 2010). More interestingly, this approach has the potential to identify the expected impacts of weed community shifts on the functionality of agroecosystems (Garnier and Navas, 2012). For instance, shifts in weed communities may result in changes in the competiveness against crops as well as in certain services that weeds provide, such as the provision of food for beneficial fauna.

In this study, we aim to evaluate whether the tillage system (conventional compared with reduced tillage) affects weed communities and their functional attributes in a predictable way, which in turn may affect the relationship of the weed flora to crop production. We analysed data on weed communities from seven European on-going trials assessing the effects of the tillage system within the framework of the TILMAN-ORG project (www.tilman-org.net). We hypothesised that (i) the type of tillage will affect weed species richness and community composition, and (ii) that these changes will lead to weed communities with different traits in response to the disturbance. These changes in weed community may have important consequences in relation to crop-weed competition and the management of agricultural systems.

## 2. Material and methods

### 2.1. Data sets

We used data from seven on-going organic or low-input field trials testing for the effect of reduced tillage practices on weed flora, within the framework of the CORE-organic TILMAN-ORG project.

**Table 1**
Data on the environmental conditions, crop types, tillage system and weed sampling of the seven field trials included in the study.

| Country | Temperature and rainfall (annual mean) | Soil type | Tillage system (depth) | Crops | Weed sampling (samples per plot) | Timing of sampling (days after sowing) | Other factors |
|---|---|---|---|---|---|---|---|
| Austria | 8.8 °C | Silty loam | Con: mouldboard plough (25 cm) | 2012 Winter wheat | Two 1 $m^2$ | 244 | – |
| | 500 mm | | Red: chisel plough (5–7 cm) | 2013 Sugar beet | Four 1 $m^2$ | 146 | |
| France | 10.3 °C | Sandy | Con: mouldboard plough (30 cm) | 2012 Winter wheat | Eight 0.25 $m^2$ | 247 | – |
| | 830 mm | | Red: chisel plough (15 cm) | 2013 Maize | | 190 | |
| Italy | 15 °C | Loam | Con: mouldboard plough (30 cm) | 2012 Sunflower | Two 4 $m^2$ | 122 | Fertilisation |
| | 826 mm | | Red: chisel plough (30 cm) | 2013 Winter wheat | Two 1 $m^2$ | 227 | |
| Luxembourg | 9.1 °C | Loamy | Con: mouldboard plough (15–25 cm) | 2012 Spring oat | Two 1 $m^2$ | 170 | Green |
| | 800 mm | sand | Red: disc harrow (5 cm) | 2013 Spring wheat | | 115 | manures |
| Netherlands | 9.5 °C | Light clay | Con: mouldboard plough (25 cm) | 2012 Spring wheat | Eight 0.25 $m^2$ | 86 | – |
| | 775 mm | | Red: cultivation (12 cm) | 2013 White cabbage | | 107 | |
| Spain | 14.9 °C | Loamy | Con: mouldboard plough (20 cm) | 2012 Spelt | Four 1 $m^2$ | 176 | Fertilisation |
| | 650 mm | clay | Red: chisel plough (20 cm) | 2013 Chickpea | | 94 | Green manures |
| Switzerland[a] | 8.9 °C | Clay | Con: mouldboard plough (15 cm) | 2010 Sunflower | One 64 $m^2$ | 83 | Fertilisation |
| | 1000 mm | | Red: chisel (5–7 cm), occasionally at 15 cm or stubble cleaner (5–7 cm) | 2011 Spelt | | 258 | |

Weed cover for each species was recorded in all of the trials with the exception of the Netherlands, where density was recorded. When only one of the sampling strategies is reported, it was the same for both crops.
[a] Data from 2010 and 2011 were used because a grass clover crop was grown in 2012 and 2013.

The trials were located in Austria (AU), France (FR), Italy (IT), Luxembourg (LUX), Netherlands (NL), Spain (SP) and Switzerland (CH), covering a wide range of environmental conditions (Table 1). The climate ranges from the Pannonian steppic part of Europe, with cold winters and dry hot summers (AU) to the Atlantic central, with a moderate climate where the average winter temperature does not go far below 0 °C and the average summer temperatures are relatively low (CH, LUX, NL), to the Mediterranean north and south (IT and SP respectively), with short precipitation periods and long hot, dry summers. The climate of the FR site is intermediate between the Atlantic and Mediterranean, with a relatively humid Atlantic climate with Mediterranean-like distribution of precipitation within a year (maximum in winter) (Metzger et al., 2005). Despite the wide range of soil texture of experimental sites (Table 1), most of them are calcareous, except LUX where bedrock is siliceous. All trials relied on an arable crop rotation with no leys, except NL. Fertilization was based on farmyard manure and/or compost, except LUX that relied only on green manuring. Crop residues were buried or used as mulch, except in CH, where they were exported. Six of seven trials were organically managed, where weed control was performed mechanically. However, IT was a low-input trial, where weeds were controlled by herbicides and chemical fertilizer applied. Although the individual results may vary depending on the specific management of each trial, our study aims to contrast a general hypothesis about the effect of reduced tillage on weed community composition and diversity, and the functional attributes by combining the information of the trials using a meta-analytic approach avoiding pooling raw data from each trial (Zaykin, 2011).

For each trial, we selected weed data from two consecutive years, and thus a total of 14 weed data sets were analysed. Although each trial had a different experimental design and/or involved different factors, all of them had in common the comparison of tillage systems, such as inversion (hereafter, conventional tillage), compared with non-inversion tillage or very shallow inversion (reduced tillage) as the main factor (Table 1). Conventional tillage consisted in mouldboard ploughing in all trials (Table 1), while different machinery (chisel plough, disc harrow and cultivator) were used for reduced tillage. The tillage depth varied between trials depending on the soil features and the farming system design. For each trial, weeds were surveyed after post-emergence weed control and the percentage of cover was recorded for each individual species, with the exception of The Netherlands trial, where weed density (the number of individuals) was recorded instead of cover (Table 1).

### 2.2. Selection of traits

Plant functional traits were selected based on the literature of functional responses to management and their potential agronomic and/or ecological role (Appendix A in Supplementary data, and relevant literature therein). The values of the different traits were obtained from open databases and specialized books and supplemented with data found in specific papers (Appendix A in Supplementary data). The analysed traits were life form (annuals versus perennials), specific leaf area (SLA, $mm^2\,mg^{-1}$), seed weight (mg), canopy height (m, maximum height at maturity), seed bank longevity (short-term, i.e., between 1–5 years, and long-term, i.e., longer than 5 years), soil nutrient condition affinity (Ellenberg and Pignatti values), beginning of flowering (month of the first flowering) and flowering span (duration of flowering in months).

### 2.3. Statistical analyses

Community-level weighted mean of trait values (CWM), which measures the weighted average of traits for the species pool in the weed community, was calculated for each single trait and for each trial and crop using package “FD” (Laliberté et al., 2014) for R (R Development Core Team, 2014). This community-aggregated metric represents the expected functional trait value of a random community sample, often representing the dominant trait value in a community. Canopy height, seed weight and SLA were log-transformed to homogenize the weight across taxa. Because the beginning of flowering was a circular variable, an angular transformation was applied to linearize it.

The effect of the tillage system on the CWM of each trait was then analysed through linear mixed-effect models. Random effects factors were included according to the experimental design of each trial. When other factors apart from the tillage system were present (Table 1), they were included in the model to account for the effect of these confounding factors. For categorical traits, we only analysed one of the levels, i.e., we analysed the CWM of the perennial weeds for life form and the CWM of the long-term seeds for the longevity of the seedbank.

The CWM was also calculated for each trial using the weed data of the two crops, and the same analyses were then performed including the crop type as a fixed effect factor to test the effect of the crop (wheat or spelt vs. other) on the CWM.

Data were transformed when necessary to meet the normality and homoscedasticity requirements. All of the analyses were performed in R 3.0.2 (R Development Core Team, 2014) with the “lme4” package (Bates et al., 2008) for mixed models and “lmerTest” to calculate the confidence intervals and the significance of the effects (Kuznetsova et al., 2014).

We also analysed the effect of the tillage system on the weed species richness and on the community composition. We performed non-metric multidimensional scaling (NMDS), a dimension reduction method that maps the differences in community composition between samples into a reduced set of axes. The Jaccard metric was used to compute the distances between plots according to their weed community composition. The first axis was used as a surrogate of the community composition. The NMDS was performed using the R package “vegan” (Oksanen et al., 2013). The effect of the tillage system on the community composition and species richness was analysed for each trial and crop using the same models as for the analyses of the CWM.

Because the raw data from each trial could not be pooled to test for a general effect of the tillage system on the functional traits of the weed communities surveyed, we used a meta-analytic approach to combine the information of the trials based on *P*-values, which is nearly as powerful as that based on combining data (Zaykin, 2011). Combined *P*-values can be used to support a common hypothesis tested in all studies, and a series of non-significant results may collectively suggest significance. We used the weighted *Z*-test, which is the Stouffer’s method (also known inverse normal test), with weights:

$$p_z = 1 - \Phi\left(\frac{\sum_{i=1}^{k} w_i Z_i}{\sum_{i=1}^{k} w_i^2}\right)$$

where $Z_i = \Phi^{-1}(1\text{-}p_i)$; $p_i$ is the *P*-value from the *i*-th study out of *k* studies in total; $w_i$ is the weight of the study; and $\Phi$ and $\Phi^{-1}$ denote the standard normal cumulative distribution function and its inverse. We used the inverse of the estimated standard error as weights, as recommended in Zaykin (2011). Then, the individual *P*-values were converted to one-sided *P*-values (always testing the same alternative hypothesis) before combining them as follows:

$p_{\text{one-sided}} = p_{\text{two-sided}}/2$ if effect direction is positive and $p_{\text{one-sided}} = 1 - p_{\text{two-sided}}/2$, otherwise.

**Table 2**
Coefficients and their *P*-values from the linear mixed models on the effect of the tillage system, i.e., conventional compared with reduced tillage, on weed community composition and diversity for each trial and crop analysed.

| Country | Crop | Community composition | | Weed species richness | |
|---|---|---|---|---|---|
| | | Estimate | *P*-value | Estimate | *P*-value |
| Austria | Winter wheat | −1.701 ± 0.259 | **0.003** | −1.400 ± 1.123 | 0.280 |
| | Sugarbeet | −0.262 ± 0.200 | 0.261 | 0.200 ± 0.548 | 0.724 |
| France | Winter wheat | −1.689 ± 0.249 | **0.003** | −4.344 ± 0.475 | **0.001** |
| | Maize | −2.261 ± 0.207 | <**0.001** | −2.766 ± 0.580 | < **0.001** |
| Italy | Winter wheat | 0.330 ± 0.163 | ***0.097*** | 0.313 ± 0.758 | 0.683 |
| | Sunflower | 0.647 ± 0.140 | <**0.001** | 0.063 ± 0.309 | 0.841 |
| Luxembourg | Spring wheat | −0.238 ± 0.067 | **0.002** | −0.125 ± 0.576 | 0.830 |
| | Spring oat | 0.604 ± 0.154 | **0.028** | −0.976 ± 0.680 | 0.244 |
| Netherlands | Spring wheat | 1.587 ± 0.286 | **0.012** | −0.441 ± 0.148 | **0.025** |
| | Cabbage | 0.148 ± 0.219 | 0.547 | −0.500 ± 0.540 | 0.390 |
| Spain | Spelt | −0.331 ± 0.148 | 0.114 | 3.000 ± 1.194 | **0.046** |
| | Chickpea | −0.319 ± 0.223 | 0.213 | 0.313 ± 0.653 | 0.649 |
| Switzerland | Spelt | −1.938 ± 0.193 | **0.013** | −0.500 ± 1.020 | 0.681 |
| | Sunflower | −2.303 ± 0.118 | <**0.001** | −0.628 ± 0.106 | **0.027** |

*P*-values below 0.05 are in bold and below 0.1 in italics.

Once they were combined, the results were converted back to two-sided as follows:

$p_{\text{two-sided}} = 2 \times p_{\text{one-sided}}$ if $p_{\text{one-sided}}$ is lower than 0.5, and $2 \times (1 - p_{\text{one-sided}})$, otherwise.

The weighted *Z*-test assumes independence among the *P*-values combined. As the two years of each trial were not totally independent, we only combined the *P*-values of the effect of the tillage system in the analyses that included both crops, i.e., one *P*-value for each trial.

## 3. Results and discussion

### 3.1. Effect of the tillage system on weed diversity and composition

In total, 99 weed species were recorded across all trials. Mean ± standard error species richness was 18.36 ± 1.88, with a minimum of 9 species found in the Netherlands in the cabbage crop and a maximum of 30 species found in Luxembourg in the oat crop. There was a broad variation in weed community composition between trials (Appendix B in Supplementary data).

The effect of the type of tillage on weed species richness differed according to the trial and the crop (Table 2; Appendix C in Supplementary data), although we observed an increasing trend in weed richness under reduced tillage compared with conventional tillage (nine out of the fourteen estimated effects of conventional tillage on weed species richness were negative). The increase in species richness was statistically significant at least in one of the two crop types in four out of the seven trials, and in one trial in both crop types (Table 2). Both positive and negative results on the effect of reducing tillage intensity on weed diversity have been previously reported (Armengot et al., 2015; Carter and Ivany, 2006; Fried et al., 2012; Hernandez Plaza et al., 2011; Santín-Montanyá et al., 2013).

We also found a clear effect of the type of tillage on the weed community composition (Table 2). In all trials except for Spain, weed assemblies were significantly affected by the type of tillage, and in many cases for both analysed crop types, which agrees with previous studies (Armengot et al., 2015).

### 3.2. Effect of the tillage system on species functional traits

The effect of the tillage system on the CWM of the selected functional traits depended on the trial and on the crop, i.e., the observed differences were not consistently significant across experiments (Table 3; Appendix C in Supplementary data). However, the results of the meta-analysis across trials showed significant differences of the tillage system on seed weight, canopy height, beginning flowering, nutrient affinity and life form but not for SLA, flowering span and longevity of the seeds in the soil seedbank (Table 4). Weed communities surveyed under conventional tillage had lower abundance of perennials, heavier seeds, were taller, flowered later and had higher affinity for nutrient-rich soils compared with those surveyed under reduced tillage (Table 4). Mouldboard ploughing buries seeds by inverting soil layers. Therefore, large seeds, which have more reserves, are favoured under conventional tillage because they have greater success in emerging from burial than the small ones (Gardarin et al., 2009). On the contrary, under reduced tillage, emergence is not constrained by the size of seeds because most of them are recruited from or are close to the soil surface (Gruber and Claupein, 2009). Moreover, small seeds are produced in larger quantities (Moles and Westoby, 2006), which may increase the abundance of small seeded species under reduced tillage.

Seed weight is also related to the persistence of the seeds in the soil seedbank (Fenner and Thompson, 2005; Peco et al., 2003); small seeds tend to persist in the soil whereas most large seeds are transient. However, our results do not support this relationship because weed communities under conventional tillage with heavier seeds were not significantly less long-lived in the seedbank (Table 4). Albrecht and Auerswald (2009) did not find this relationship in arable fields either. The seedbank is the primary source of new infestations of annual weeds each year, and thus, the long-term persistence of seeds may increase the abundance of seeds in the soil and promote high infestations. According to our results, the reported differences in weed infestation between

**Table 3**
Coefficients (estimate ± standard error) and their *P*-values from the linear mixed models on the effect of the tillage system (conventional compared with reduced tillage) on the Community Weighted Mean values of the functional attributes of weed communities for each trial and crop analysed.

| Country | Crop | Community Weighted Mean values of traits | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Seed weight | | Canopy height | | Specific leaf area | | Beginning flowering | | Flowering span | | Nutrient affinity | | Life form | | Seedbank longevity | |
| | | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value |
| Austria | Winter wheat | 0.274 ± 0.232 | 0.303 | 0.222 ± 0.061 | **0.022** | −0.012 ± 0.027 | 0.681 | 0.377 ± 0.054 | **0.002** | 0.676 ± 0.182 | **0.006** | 1.588 ± 0.327 | **0.008** | −0.455 ± 0.095 | **0.009** | −0.034 ± 0.030 | 0.317 |
| | Sugarbeet | 0.340 ± 0.060 | **0.005** | 0.220 ± 0.088 | **0.038** | −0.022 ± 0.039 | 0.600 | 0.224 ± 0.052 | **0.012** | 0.166 ± 0.138 | 0.275 | −0.322 ± 0.093 | **0.009** | −0.119 ± 0.052 | ***0.084*** | 0.004 ± 0.016 | 0.812 |
| France | Winter wheat | 0.273 ± 0.146 | 0.139 | 0.262 ± 0.062 | **0.013** | N | | 0.050 ± 0.022† | ***0.082*** | −0.818 ± 0.371 | ***0.093*** | 0.118 ± 0.671 | 0.869 | N | | −0.252 ± 0.065 | **0.001** |
| | Maize | −0.147 ± 0.065 | **0.035** | 0.101 ± 0.063 | 0.181 | 0.169 ± 0.070 | ***0.071*** | 0.095 ± 0.016 | **0.004** | 0.430 ± 0.153 | **0.049** | 1.268 ± 0.442 | **0.047** | N | | −0.043 ± 0.118 | 0.733 |
| Italy | Winter wheat | 0.702 ± 0.291 | **0.024** | 0.802 ± 0.170 | <**0.001** | 0.061 ± 0.035 | ***0.090*** | 0.078 ± 0.100 | 0.438 | 0.224 ± 0.086 | **0.016** | 0.024 ± 0.174 | 0.892 | −0.244 ± 0.060 | <**0.001** | 0.115 ± 0.019 | <**0.001** |
| | Sunflower | 1.145 ± 0.308 | **0.001** | 0.801 ± 0.145 | <**0.001** | −0.013 ± 0.032 | 0.685 | 0.074 ± 0.047 | 0.134 | 0.093 ± 0.096 | 0.341 | 1.358 ± 0.250 | <**0.000** | −0.346 ± 0.066 | **0.001** | 0.027 ± 0.007 | **0.001** |
| Luxembourg | Spring wheat | −0.181 ± 0.037 | <**0.001** | −0.010 ± 0.033 | **0.004** | −0.024 ± 0.021 | 0.335 | −0.050 ± 0.044 | 0.341 | 0.128 ± 0.140 | 0.370 | 0.487 ± 0.213 | ***0.062*** | −0.081 ± 0.026 | **0.004** | −0.024 ± 0.009 | **0.012** |
| | Spring oat | 0.193 ± 0.078 | ***0.087*** | 0.077 ± 0.060 | 0.289 | −0.012 ± 0.013 | 0.433 | −0.068 ± 0.032 | **0.041** | 0.244 ± 0.147 | 0.110 | −0.119 ± 0.085 | 0.174 | −0.156 ± 0.050 | **0.050** | −0.003 ± 0.009 | 0.722 |
| Netherlands | Spring wheat | 0.078 ± 0.038 | 0.136 | 0.010 ± 0.002 | 0.251 | −0.084 ± 0.044 | 0.154 | 0.322 ± 0.147 | 0.117 | −1.281 ± 0.601 | 0.123 | −0.144 ± 0.099 | 0.244 | 0.176 ± 0.090 | 0.145 | 0.001 ± 0.002 | 0.698 |
| | Cabbage | −0.120 ± 0.022 | **0.026** | −0.013 ± 0.017 | 0.490 | −0.008 ± 0.030 | 0.806 | 0.003 ± 0.016 | 0.877 | 0.049 ± 0.123 | 0.705 | 0.158 ± 0.117 | 0.271 | −0.041 ± 0.011 | **0.035** | −0.008 ± 0.004 | 0.173 |
| Spain | Spelt | −0.000 ± 0.022 | 0.987 | −0.042 ± 0.061 | 0.530 | −0.018 ± 0.010 | ***0.081*** | −0.003 ± 0.022 | 0.884 | 0.079 ± 0.272 | 0.797 | 0.392 ± 0.280 | 0.353 | 0.004 ± 0.060 | 0.948 | −0.002 ± 0.010 | 0.821 |
| | Chickpea | 0.257 ± 0.343 | 0.487 | 0.150 ± 0.058 | ***0.058*** | −0.018 ± 0.008 | **0.049** | 0.201 ± 0.136 | 0.203 | −1.070 ± 0.636 | 0.159 | −0.194 ± 0.472 | 0.709 | −0.089 ± 0.064 | 0.223[a] | 0.018 ± 0.020 | 0.420 |
| Switzerland | Spelt | 0.243 ± 0.510 | 0.689 | 0.001 ± 0.027 | 0.969 | −0.026 ± 0.012 | 0.172 | 0.355 ± 0.200 | 0.216 | 1.981 ± 0.415 | ***0.052*** | −0.197 ± 0.332 | 0.618 | −1.245 ± 0.435 | 0.118[b] | 0.024 ± 0.011 | 0.163 |
| | Sunflower | 0.642 ± 0.518 | 0.369 | 0.152[b] ± 0.223 | 0.566 | N | | 0.534 ± 0.323 | < **0.001** | −1.249 ± 0.343 | ***0.068*** | −0.468 ± 0.755 | 0.601 | −0.103 ± 0.111 | 0.481 | 0.045 ± 0.023 | ***0.058*** |

*P*-values below 0.05 are in bold and below 0.1 are in italics. 'N' stands for non-normal data, which could not be analysed.
Nutrient affinity was approximated using Ellenberg and Pignatti values. Life form stands for perennial weeds and seedbank longevity stands for the long-term persistence of seeds in the soil (longer than 5 years).
[a] Log-transformation.
[b] Square root transformation.

**Table 4**
Coefficients (estimate ± standard error) and their *P*-values from the linear mixed models on the effect of the tillage system, i.e., conventional compared with reduced tillage, on the Community Weighted Mean values of the functional attributes of weed communities for each trial, after subtracting the effect of crop.

| CWM | Community Weighted Mean values of traits<br>Seed weight | | Canopy height | | Specific leaf area | | Beginning flowering | | Flowering span | | Nutrient affinity | | Life form | | Seedbank longevity | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Country | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value |
| Austria | 0.206 ± 0.080 | **0.021** | 0.221 ± 0.055 | **0.001** | −0.017 ± 0.025 | 0.501 | 0.301 ± 0.047 | <**0.001** | 0.290 ± 0 .217 | 0.206 | 0.633 ± 0.300 | **0.049** | −0.287 ± 0.071 | **0.001** | −0.002 ± 0.014 | 0.905 |
| France | 0.089 ± 0.094 | 0.372 | 0.118 ± 0.085 | 0.200 | 0.098 ± 0.062 | 0.147 | 0.023 ± 0.025 | 0.400 | −0.115± 0.299 | 0.713 | 0.494 ± 0.403 | 0.260 | 0.087 ± 0.085 | 0.411 | −0.168 ± 0.082 | 0.111 |
| Italy | 0.924 ± 0.210 | <**0.001** | 0.801 ± 0.111 | <**0.001** | 0.013 ± 0.020 | 0.537 | −0.030 ± 0.043 | 0.501 | N | | 0.691 ± 0.176 | <**0.001** | −0.295 ± 0.045 | <**0.001** | 0.069 ± 0.013 | <**0.001** |
| Luxembourg | 0.017 ± 0.047 | 0.720 | −0.013 ± 0.029 | 0.655 | −0.016 ± 0.010 | 0.120 | −0.018 ± 0.021 | 0.416 | −0.244± 0.121 | **0.049** | 0.187 ± 0.095 | ***0.054*** | −0.117 ± 0.027 | <**0.001** | −0.118 ± 0.007 | **0.044** |
| Netherlands | 0.004 ± 0.036 | 0.924 | −0.020 ± 0.016 | 0.913 | N | | 0.110 ± 0.105 | 0.306 | −0.281± 0.300 | 0.370 | 0.007 ± 0.126 | 0.957 | 0.067 ± 0.071 | 0.366 | −0.004 ± 0.003 | 0.275 |
| Spain | 0.129 ± 0.214 | 0.569 | 0.054 ± 0.049 | 0.319 | −0.018 ± 0.007 | **0.014** | 0.099 ± 0.077 | 0.221 | −0.500± 0.407 | 0.280 | 0.099 ± 0.315 | 0.795 | −0.028 ± 0.038 | 0.476 | 0.008 ± 0.009 | 0.395 |
| Switzerland | 0.443 ± 0.109 | <**0.001** | 0.081 ± 0.098 | 0.497 | N | | 0.444 ± 0.087 | **0.038** | N | | −0.332 ± 0.458 | 0.550 | −0.336 ± 0.098 | ***0.085*** | 0.029 ± 0.028 | 0.419[a] |
| Weighted Stouffer's test | | <**0.001** | | <**0.001** | | 0.24 | | **0.002** | | 0.174 | | **0.002** | | <**0.001** | | 0.546 |

The weighted Stouffer's test combines the information of *P*-values to test for a common hypothesis across trials (refer to the text for more details).
*P*-values below 0.05 are in bold and below 0.1 are in italics. 'N' stands for non-normal data, which could not be analysed.
Nutrient affinity was approximated using Ellenberg and Pignatti indicator values. Life form stands for perennial weeds, and seedbank longevity stands for the long-term persistence of seeds in the soil (longer than 5 years).
[a] Square root transformation.

**Table 5**
Coefficients (estimate ± standard error) and their *P*-values from the linear mixed models on the effect of the crop type on the Community Weighted Mean values of the functional attributes of weed communities for each trial and crop analysed after subtracting the effect of the tillage system.

| CWM | Seed weight | | Canopy height | | Specific leaf area | | Beginning flowering | | Flowering span | | Nutrient affinity | | Life form | | Seedbank longevity | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Country | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value | Estimate | *P*-value |
| Austria | 0.675 ± 0.080 | <**0.001** | 0.451 ± 0.055 | <**0.001** | −0.131 ± 0.025 | <**0.001** | 0.634 ± 0.047 | <**0.001** | −1.324 ± 0.217 | <**0.001** | −1.711 ± 0.300 | <**0.001** | 0.509 ± 0.071 | <**0.001** | −0.002 ± 0.014 | 0.865 |
| France | 0.304 ± 0.094 | **0.014** | 0.241 ± 0.085 | **0.020** | −0.100 ± 0.062 | 0.142 | −0.100 ± 0.025 | **0.007** | −0.344 ± 0.299 | 0.287 | −1.896 ± 0.403 | **0.002** | −0.020 ± 0.040 | 0.635 | 0.063 ± 0.053 | 0.290 |
| Italy | 0.061 ± 0.210 | 0.772 | −0.619 ± 0.111 | <**0.001** | 0.014 ± 0.020 | <**0.001** | −0.134 ± 0.043 | **0.003** | N | | −1.418 ± 0.176 | <**0.001** | −0.054 ± 0.045 | 0.234 | −0.150 ± 0.013 | <**0.001** |
| Luxembourg | −0.145 ± 0.047 | **0.003** | −0.008 ± 0.029 | 0.800 | 0.080 ± 0.010 | <**0.001** | −0.189 ± 0.021 | <**0.001** | 0.664 ± 0.121 | <**0.001** | −0.194 ± 0.095 | **0.047** | −0.135 ± 0.027 | <**0.001** | −0.025 ± 0.007 | <**0.001** |
| Netherlands | 0.169 ± 0.036 | <**0.001** | 0.089 ± 0.016 | <**0.001** | N | | 0.870 ± 0.105 | <**0.001** | −2.492 ± 0.300 | <**0.001** | 0.364 ± 0.126 | **0.016** | 0.562 ± 0.071 | <**0.001** | −0.004 ± 0.003 | 0.220 |
| Spain | 1.492 ± 0.099 | <**0.001** | 0.127 ± 0.042 | **0.005** | 0.025 ± 0.007 | **0.001** | 0.389 ± 0.052 | <**0.001** | −2.069 ± 0.266 | <**0.001** | −0.978 ± 0.137 | <**0.001** | 0.242 ± 0.036 | <**0.001** | −0.073 ± 0.009 | <**0.001** |
| Switzerland | −0.692 ± 0.109 | <**0.001** | 0.482 ± 0.034 | <**0.001** | N | | 0.036 ± 0.037 | 0.329 | N | | 1.162 ± 0.114 | <**0.001** | −0.043 ± 0.054 | 0.425 | 0.142 ± 0.010 | <**0.001**[a] |

*P*-values below 0.05 are in bold. 'N' stands for non-normal data, which could not be analysed.
Crop type compares the crops included in the two years of the experiments being analysed. Nutrient affinity was approximated using Ellenberg and Pignatti indicator values. Life form stands for perennial weeds, and seedbank longevity stands for the long-term persistence of seeds in the soil (longer than 5 years).
[a] Square root transformation.

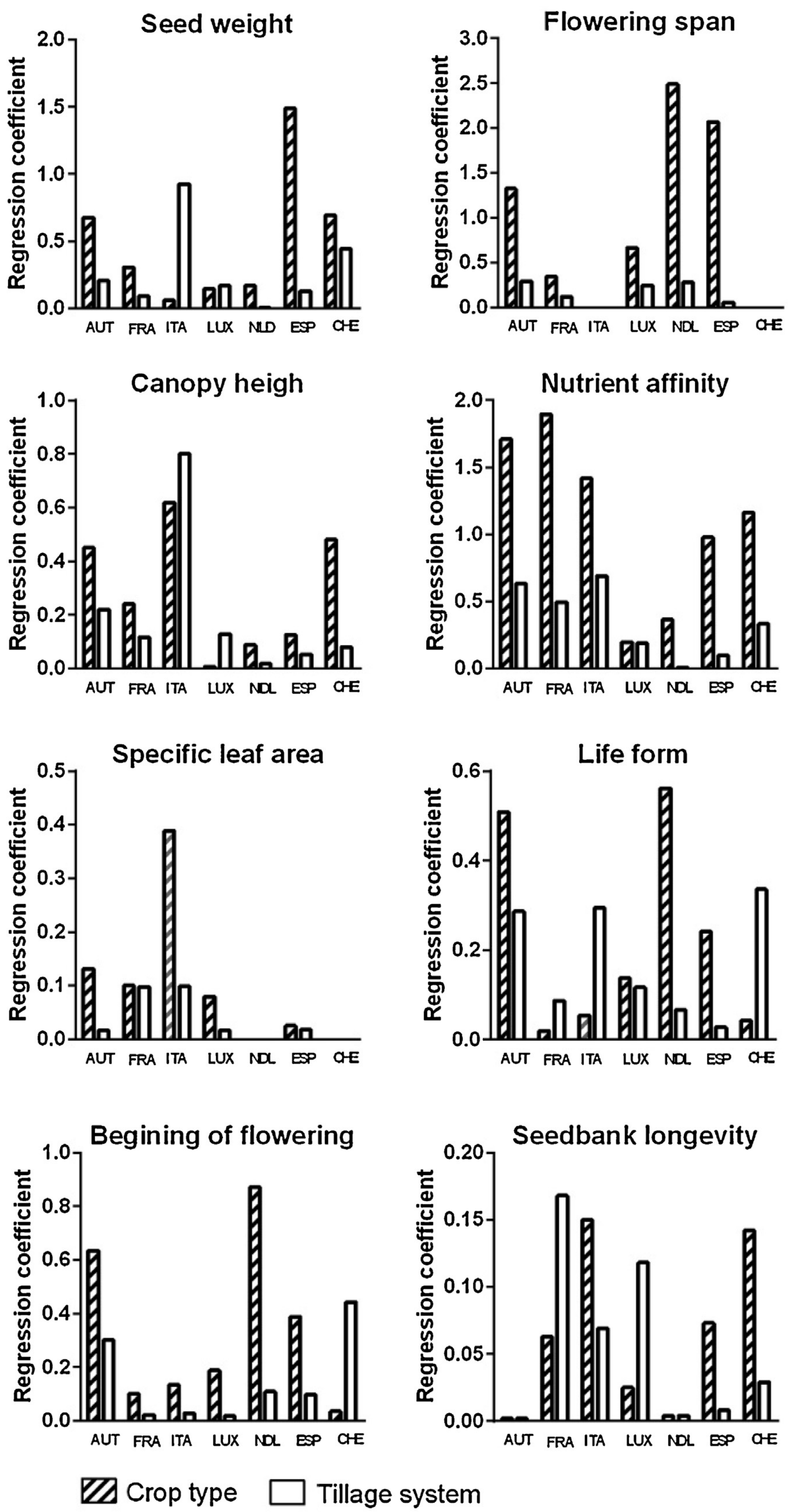


**Fig. 1.** Relative importance (absolute value of the regression coefficients from the lineal mixed models) of the tillage system and crop type on the community weight of mean values of the different functional traits of the weed communities.

tillage systems are not related to the potential persistence of the seeds, as we did not find differences in the long-term viability of seeds of the weed communities surveyed in both tillage systems (Armengot et al., 2015; Légère et al., 2013; Vakali et al., 2011).

Canopy height is closely linked with the competitive ability of the plants because the taller ones can better compete for the light with neighbouring plants. Our results showed that weed communities under conventional tillage were taller than under reduced tillage (Table 4). Thus, weed communities are potentially more competitive under conventional tillage, which could be a threat for crop production. In this sense, differences in the competitiveness of the weed communities may partially explain that in some experiments, crop yields under reduced tillage were similar to those under conventional tillage, even though total weed abundance was higher under reduced tillage (e.g., Armengot et al., 2015). However, Fried et al. (2012) found the opposite trend in a large-scale weed survey conducted in France, because in their study shorter plants with small seeds and early flowering were associated with intensive tillage practices, assessed by the tillage depth and the number of tillage passages. Fried et al. (2012) argue that these weed traits are typical features of weed species that face recurrent disturbance. However, in our study the primary source of variation was the soil inversion, because the timing of the tillage was the same in both systems in each experiment.

The higher abundance of perennials found in weed communities under reduced tillage can also pose a serious threat to crop production, as they are more difficult to control than annual species (Tables 3 and 4). The growth of perennial weeds with creeping roots or rhizomes is favoured by the reduction of the tillage intensity, but the shallow tillage with tine or discs used under reduced tillage can also promote their growth by dispersing the rhizomes (Peigné et al., 2007). Higher abundance of perennials under reduced tillage is a common result in most of the long-term experiments and large-scale surveys (e.g., Armengot et al., 2015; Fried et al., 2012). New weed control strategies are then crucial to reduce the weed pressure under this tillage system.

Perennial species usually have lower values of SLA (Garnier et al., 1997), as they have longer life spans and can invest more resources in structural tissues and defensive compounds. However, our results did not reveal significant differences between tillage systems (Table 4). SLA highly determines the assimilation rates, and it is of great interest to distinguish different strategies for weed resource use (Storkey, 2005). However, Fried et al. (2012) did not find clear relationships between SLA and farming practices and concluded that SLA may not be a good predictor of changes in agricultural management.

Weed communities under conventional tillage showed higher values of nutrient soil affinity (higher Ellenberg and Pignatti values) compared with those found under reduced tillage systems (Table 4). This may be related to the fact that mineralisation of soil organic matter is slowed compared to conventional tillage, which may result in a nitrogen shortage (Berner et al., 2008; Peigné et al., 2007). Then, weeds with low nutrient requirements may be favoured under reduced tillage. Trichard et al. (2013) did not observe changes in the nitrogen ecological requirements of weeds when comparing no-till with till systems. However, the study was performed in conventional fields and they argue that the lack of differences was most probably because the level of mineral nitrogen availability was controlled by the farmers using synthetic fertilisers. In our study, the higher affinity of weeds for nitrogen found under conventional tillage may also indicate that they can better compete with the crop for the nutrient resources than those found in reduced tillage systems, which could also have negative effects on the crop production.

Among the phenological traits, the tillage system affected the flowering onset but not the flowering span (Table 4). Both traits have been shown to be relevant in studying the responses of weeds to the timing and frequency of disturbances (Gaba et al., 2014), but it remains unclear how they are affected by different tillage systems. Opposite results on the effect of reduced and conventional tillage systems on the flowering onset have been reported (e.g., Fried et al., 2012; Trichard et al., 2013), which may be related to differences in crop sowing dates between tillage systems in each study and then to potentially different weed communities. In our experiments, where timing of the agricultural practices were the same between both tillage systems in each experiment, weed communities of conventional tillage fields flowered later than those under reduced tillage. A better understanding of the changes in phenology is of major relevance because they are closely linked and may modify the presence or abundance of other taxa that depend on flower availability (Brooks et al., 2012; Storkey et al., 2013). Moreover, the onset of flowering determines the seed production; later flowering usually leads to lower seed production (Fried et al., 2012; Storkey, 2006). This trait may thus be relevant for predicting future weed infestations.

### *3.3. Effect of the crop type on the functional characteristics of weed communities*

Several studies have revealed the major importance of the crop type on weed community composition (Armengot et al., 2015; Fried et al., 2008) and also on its functional composition (Gunton et al., 2011). Crop type includes the effect of sowing season, fertilisation regimes, architecture and height of crop species, row spacing, and weeding types and strategies that may both constrain the taxonomical and functional composition of the weed communities. For instance, Gunton et al. (2011) found a strong relationship between the crop sowing date and the onset of weed flowering.

In our study, we found a significant effect of the crop on the CWM of all the analysed functional traits for most of the trials (Table 5). The effect of the different crops on the CWM is not discussed here in detail because it was not the objective of the study, as different crops and varieties were sown in each trial, particularly among summer crops. In general, weed communities of wheat or spelt crops compared with their counterparts had higher values of seed weight, canopy height and SLA, flowered later and for shorter periods, and had less ecological affinity for nutrient resources (Table 5). However, it is worth highlighting that the crop type significantly affected the CWM values in a higher number of trials than did the tillage system for all of the analysed traits (Tables 3 and 4). In addition, when we compared the size of the effect of both the crop and the tillage system on the CWM values, we observed that the crop type had a higher effect size in more than 80% of the cases evaluated (Fig. 1). As crop has a strong effect on weed community traits, it could be that the detected differences between tillage systems are, in part, crop-mediated responses. Crop establishment and growth (height and canopy development) may also respond to tillage (Verhulst et al., 2011), and thus some effects of tillage may be indirect through the interaction with crop.

## 4. Conclusions

Our study, which deals with two years of data of seven on-going trials in different climatic regions of Europe, reinforces the previous knowledge on the effect of the tillage system on weed community composition. However, most importantly, it provides solid evidence of the consequences of these changes on the functional attributes of the communities and their potential consequences from a mainly agronomic point of view. The tillage system affected the functional attributes of the weed communities; the CWM of all of the traits evaluated differed between tillage systems except for the SLA, the flowering span and the longevity of the seedbank. However, none of the weed communities found in the two tillage systems reunite all of the ideal attributes to diminish weed-crop competition. Instead, weed functional trait values favourable to crop production were found under both tillage systems. For instance, weed communities of reduced tillage systems were potentially less competitive because they were shorter and had less affinity for nutrients. However, under conventional tillage, the potentially lower seed production because of the higher weight of the seeds, the later flowering, and the lower abundance of perennials are traits that may reduce the weed-crop competition.

Although our study strongly supports the relevant role of the tillage system on the functional attributes of the weed communities, it is noteworthy that the crop choice is the main driver of the shifts in the functional composition of the weed communities.

Still, further studies are necessary to disentangle the effects of the changes on the functional attributes of the weed communities from an ecological point of view and mainly on the interactions with other trophic levels.

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## Appendices. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.02.021.

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