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Functional shifts in weed community composition following adoption of conservation agriculture

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Abstract:

To better understand the changes in weed communities following the adoption of conservation agriculture (CA), we investigated the functional composition of weed communities in fields implementing CA continuously from 1 to 21 years.

Weed surveys were conducted in 100 winter wheat fields of 53 farmers in the Bourgogne-Franche-Comté region, Eastern France. Ten response traits were selected to highlight changes in the functional composition of weed communities, using weighted mean value for quantitative traits and an approach based on composition analysis for qualitative traits. Out of the ten traits, four were impacted by the time following the adoption of CA significantly, while two only showed trends. Specific leaf area, leaf dry matter content, seed dispersal mode and soil seedbank longevity did not change over time following adoption of CA, whereas changes were observed for plant type, Raunkiær's life forms, Ellenberg's indicator value for light and germination and flowering periods. Phanerophyte and geophyte life forms, summer-germinating species, and spring- and summer-flowering species increased with time following adoption of CA. Shade-tolerant species, not present in field recently converted to CA, established later. Community-weighted mean of seed mass and the percentage of graminoids tended to increase with time following adoption of CA. Some functional shifts in weed communities occurred quicker than others (i.e. summer-germinating species increased after at least ten years of continuous application of CA principles). These results can be used to inform farmers moving towards CA about expected changes.

KEYWORDS

Response trait, community weighted mean, community assembly processes, transition phase, no-tillage, direct seeding, field network

1 INTRODUCTION

In agroecosystems, cropping practices play a key role in assembling weed communities. Together with ecological and environmental conditions, they act as filters and shape the composition of weed communities (Booth and Swanton, 2002). Hence, viewed within a community assembly framework, drastic changes in farming practices can either constrain or promote the representation of species within the subsequent weed community. Considering that arable lands have been tilled since the industrialization of agriculture, the adoption of conservation agriculture by farmers could be considered, from a weed science point of view, as one the main evolution in cropping strategies in recent decades. Conservation agriculture (CA) changes farming systems based on the simultaneous and continuous application of three principles: minimum soil disturbance (no-tillage), permanent residue cover on the soil surface (cover crops or mulch) and a high crop rotation diversification (Reicosky, 2015).

The response of weed communities to changes in cropping practices was often studied from the taxonomic perspective (Légère et al., 2005; Fried et al., 2008). Recently, the use of functional traits has been proposed as an effective method for identifying general rules governing community assembly (Armengot et al., 2016; Gaba et al., 2017). Most studies using a functional approach have focused on the response of weed communities to the reduction in tillage intensity (Zanin et al., 1997; Armengot et al., 2016). By lowering the intensity of a major disturbance of weed community and modifying the vertical distribution of seeds in the soil (Clements et al., 1996), reduced tillage leads to the development of perennials (Zanin et al., 1997) and select for smaller seeds that can easily penetrate the soil (Armengot et al., 2016). Wind-disseminated species, known as rapid colonizers, and graminoid species seem to be favoured in no-till systems (Debaeke and Orlando, 1991; Zanin et al., 1997; Young and Thorne, 2004; Murphy et al., 2006). However, the functional responses of weed communities to CA which include two other CA principles (i.e. residue cover on the soil surface and crop rotation diversification) in addition to no-till are not as well documented (Gunton et al., 2011; Mahaut et al., 2019). By maximizing the soil coverage, farmers intend to increase the competition between sown species (crops and cover crops) and weeds (Teasdale, 1996), selecting for more competitive and shade-tolerant weeds. Since crop diversification can create also new temporal niches, one would also expect to observe a diversification of weed life cycle periods.

Of all the weed community studies conducted in CA, only Trichard et al. (2013) reported the functional responses of weed communities to the simultaneous and the

continuous application of the three CA principles during the five first years following CA adoption (for most of the fields). During these first years of CA, the authors confirmed results observed on reduced tillage systems, such as the increase in perennial and graminoid species. More recently, Derrouch et al. (2021) showed that higher functional homogeneity of weed communities occurred in CA fields only ten years after continuous application of CA. Thus, the effects of CA practices on weeds communities present in fields during the first years could be masked by a buffering effect of the seedbank whose composition is related to cultural practices carried out before the adoption of CA.

In this article, we studied the functional shifts of weed communities following the adoption of CA, analyzing the functional composition or value of ten response traits (Raunkiær's life form, soil seedbank longevity, plant type, time of flowering, time of germination, seed dispersal, Ellenberg's indicator value for light, seed mass, specific leaf area and leaf dry matter content) of weed communities surveyed in 100 winter wheat fields of 53 farmers that had been implementing CA continuously for 1 to 21 years. We hypothesized that the adoption of CA will favour the development of non-therophyte life forms, graminoids, rapid colonizers such as anemochore or zoochore species, smaller seeds and more shade-tolerant species. We hypothesized the average soil seedbank longevity of the community to decrease with time since the adoption of CA because no-till and cover crop place seeds in non-favourable conditions to germinate on the soil surface. We expected also an unfavourable filtering for species with high internal conductivity (high specific leaf area) and low investment in structural tissues (low leaf dry matter content), due to a higher competition for light. Crop rotation diversification and lack of soil disturbance during the intercropping period was expected to increase summer- and/or fall- germinating or flowering species. Finally, we expected that most of the functional shifts would be observed in fields that have been in CA for more than five years, due to the buffering effect of the weed seedbank and to an adaptation of weed management by farmers after this period, such as the inclusion of summer crops (Derrouch et al., 2020a).

2 MATERIALS AND METHODS

2.1 Study site

The study area was located in Bourgogne-Franche-Comté, a temperate oceanic zone located in the northeaster of France, where yearly rainfall and daily temperatures average 756 mm and

10.9°C, respectively (https://www.insee.fr/fr/statistiques/4176857). Based on a network of 53 farmers, we selected 100 winter wheat (*Triticum aestivum* L.) fields under annual crop production (i.e. without temporary meadows) for at least four years, that had been implementing CA continuously for one to 21 years. Fields were grouped into four groups of age since CA adoption. Age group boundaries were chosen according to the periods during which changes in weed community structure were observe (Derrouch et al., 2021) and which changes were observed in a national survey n weed management practices (Derrouch et al, 2020a). Fields of group "1" with one year of time since CA adoption (12 fields) constituted the initial state. Fields of group "2-5" had a time since CA adoption from two to five years (42 fields). Fields of group "6-10" had a time since CA adoption from six to ten years (32 fields) and represented a period during which French CA farmers generally adapt their weed management (summer crops added, shift to post-emergence herbicide application) (Derrouch et al., 2020a). Finally, the group ">10" grouped fields with a time since CA adoption more than 10 years (14 fields) and represented the period during which weed communities become significantly more similar and homogeneous (Derrouch et al., 2021). Weed management changes made during the six to ten first years of CA were retained after ten years of CA.

2.2 Weed data collection

Weed surveys were conducted in each field in 2018 (51 fields) and 2019 (49 fields) over three periods: early March (before the last post-emergent herbicide use), mid-June (before harvest), and early September (intercropping period before sowing of the following crop). In all surveys, weeds were recorded on a 40x50 m area, located 50 m away from field boundaries, following a W-shaped walked path (2 persons, 30-40 minutes for each survey). Most plants were identified at the species level and named according to French taxonomic referential (TaxRef V13, (Gargominy et al., 2019)). The genus level was used only for immature plants or because of the lack of distinguishing criteria (*e.g. Lolium* sp.). The abundance of each species was estimated according to a modified Barralis' scale (Barralis, 1976): [+] found once in the 2,000 m^2 plot; [1] less than 1; [2] 1 to 2; [3] 3 to 10; [3.5] 11 to 20; [4] 21–50 and [5] 51 to 60 individuals m^{-2}. The percentage of stage of development (seedling, vegetative, flowering, fructification) of each species was also estimated. Based on information provided by the farmers, species that were sown in the current or preceding year were not considered in the analysis, thus excluding most of cover crop species and volunteer crop plants.

To better explained the changes in community assembly processes induced by the application of CA, only weeds with a successful establishment, *i.e.* able of producing propagules or of maintaining during the crop cycle were selected (see Appendix S1 for details), selecting 226 out of the 256 weed species observed (see the full list of species with their occurrence and abundance in Table S1).

2.3 Biological traits

Based on a reference list of functional traits for arable weeds (Booth and Swanton, 2002; Gaba et al., 2017) and articles on no-till (Debaeke and Orlando, 1991; Young and Thorne, 2004; Murphy et al., 2006) and CA (Trichard et al., 2013), we selected ten responses traits. Seven were categorical: Raunkiær's life form, soil seedbank longevity (six classes), plant type (graminoid/eudicotyledon), germination and flowering periods, seed dispersal mode and Ellenberg's indicator value for light (EIV-l). Three traits were quantitative: seed mass (mg), specific leaf area ($mm^2.mg^{-1}$) and leaf dry matter content ($mg.g^{-1}$). Raunkiær's life form (Raunkiær et al., 1934), seed mass and soil seedbank longevity were related to the reduction of soil disturbances. Raunkiær's life form was used to capture the potential effect of an absence of mechanical soil disturbance on the development of non-therophytes life forms. The traits referring to seeds (seed mass and soil seedbank longevity) were used to assess the effect of a change in the vertical distribution of seeds in the soil on seed characteristics and their ability to persist in the seedbank. Plant type was selected to confirm the shift towards more graminoids species observed in the literature (Debaeke and Orlando, 1991; Trichard et al., 2013). This response trait can also be used to observe the response of weed communities to a potential change in weed management, as farmers can use herbicide specifically targeting either graminoids or eudicotyledons. The periods of germination and flowering were chosen to capture the effect of CA on temporal niches. Seed dispersal was used to assess the ability of plants to colonize fields (Benvenuti, 2007). The use of Ellenberg's indicator value for light was used to capture a potential filtering of more shade-tolerant species. The specific leaf area and the leaf dry matter content were used to capture the effect of both changing internal dynamics of communities and reducing disturbances.

All trait values were extracted from databases (Table S2 for selection details and data sources). For weed species identified at genus level, we selected the trait value of the most common species belonging to the same genus. For trees and shrubs, traits values were based on the most common species in the region (Bardet et al., 2008).

2.5 Statistical analysis

To obtain a value representative of each trait at the community level, we started by computing the community-level weighted mean (quantitative traits) or the weighted proportion (categorical traits) of trait attributes (CWM). For the seven categorical traits, we obtained the weighted proportions of each attribute. This form of data, composed of non-negative components whose sum was 1 (or 100 %) for each trait, causes some problems with classical methods of analysis based on Euclidean geometry (Jackson, 1997) and several authors have pointed out the risks of using classical methods with this type of data. So, we used the CoDa (compositional data) approach proposed by Aitchison (2003). As zero counts represented a problem for the analysis of compositional data, they were imputed according to a Bayesian paradigm proposed by Palarea-Albaladejo and Martin-Fernandez (2015) and implemented in the cmultRepl() function of the {zCompositions} package. We reported compositional descriptive statistics and variance for traits proportions as the closed geometric mean and variance matrix of centred log-ratio (clr) transformed data set. The geometric mean better represents the centre of compositional data points than the arithmetic mean, and dispersion of compositional data is summarized using a variance matrix of pairwise log-ratios (Aitchison, 2003).

Principal component analysis on clr transformed data was used to examine variance in the proportions of traits (Aitchison and Greenacre, 2002). In this analysis, the PCA axes were plotted using a biplot in which the length of the link (*i.e.*, distance between arrowheads) along a component relates to the standard deviation (SD) of the log-ratio of two components. Thus, the distance between links was used to evaluate relative variation between components. We used compositional analysis in acomp geometry as proposed by Van-den-boogaart et al. (2020) in {compositions} package.

To examine differences in traits composition between the four groups of CA adoption, we used a permutation-based MANOVA (PERMANOVA) on Euclidean distance matrix calculated on the clr-transformed data for categorical traits and Euclidean distance on the CWM values for quantitative traits. For these analysis we used the adonis() function implemented in the {vegan} package (Oksanen et al., 2019). All the analysis were done with R version 4.0.2 (R Development Core Team, 2021).

3 RESULTS

Weed communities were composed of an average of 23.9 species per 2,000 m² plot (± 12.7 SD). The most frequent species were *Taraxacum officinale* F.H.Wigg. (present in 84% of the fields), *Alopecurus myosuroides* Huds. (78%) and *Chenopodium album* L. (78%). Half of the 226 species were present in less than five fields. Most species showed low average abundance (less than one plant m^{-2} or even one plant per 2,000m^2). The most abundant species, *Veronica hederifolia* L. (7.55 plants per m^2 on average), *Digitaria sanguinalis* (L.) Scop. (7.32 plants per m^2), *Setaria pumila* (Poir.) Roem. & Schult. (6.43 plants per m^2) and *Amaranthus hybridus* L. (5.23 plants per m^2) were not the most frequent species (occurrence between 5 and 22 %) (Table S1). Some species, more commonly found in others habitats such as woodlands (*Acer* sp., *Euonymus europaeus* L., *Hedera helix* L., *Juglans* sp.), field edges (*Rubus* sp., *Heracleum sphondylium* L., *Cornus* sp.) or meadows (*Rumex obtusifolius* L., *Plantago lanceolata* L., *Plantago media* L.) were also present in weed communities.

3.1 Overall trait representation

Weed communities were mainly composed of therophyte (98 species) or hemicryptophyte (88 species). Annual weeds (71.2% of plants) were more abundant than perennials in the weed communities. Hemicryptophytes (23.1% of plants) represented most of perennial weeds (Table 1). Around half of species had a transient soil seedbank (a maximum one-year survival in the soil). These species accounted for 35.8% of plants in the weed communities. Most of the plants on weed communities (70.2%) had a seed survival in soil less than five years (transient, transient to short term and short term attributes). Only 33 species were graminoids but these species accounted for about 27% of individuals in weed communities. Slightly less than half of the weeds (42%) had a flowering period during the intercropping period (summer to autumn). Species with a spring to summer and a spring to autumn flowering period (48 and 53 species, respectively) were also well represented in weed communities (28.7% and 20.4% of individuals, respectively). About 23.6% of the weeds were able to germinate all year round. For most of the remaining weeds, germination occurred either at the beginning (autumn to spring) or at the end (spring to summer) of the winter crop. Although represented by 52 species, only 7.5% of the weeds had a spring germination period. Seed dispersal modes were fairly well distributed by species with no particular dispersion mechanisms (73 species),

anemochorous (62) and zoochorous species (83). However, considering their abundance, almost half of weeds produced seeds that remained in the field (no dispersion mechanism). Most species (195) and high percentage of weeds (88.8%) were heliophilous (Ellenberg's indicator value for light of 7, 8 or 9). Mean values for seed mass, specific leaf area and leaf dry matter content were 4.9 mg, 25.4 $mm^2.mg^{-1}$, and 187.2 $mg.g^{-1}$, respectively. Although the mean CWM values for specific leaf area and the leaf dry matter content traits were fairly stable (low coefficient of variation across communities: 12% and 14%), the mean CWM value of the seed mass was more variable across weed communities (coefficient of variation of 79%).

Table 1 near here

3.2 Functional shifts by CA age groups

Time since CA adoption appeared to have important effect on functional composition of weed communities. For categorical traits, PERMANOVA results (Table 2) identified a significant effect of time since CA adoption on the weed community composition for the Raunkiær's life form (F= 4.06, p= 0.001), the time of flowering (F= 3.422, p= 0.001), the time of germination (F= 2.719, p= 0.013) and the Ellenberg's indicator value for light (F= 3.105, p= 0.002). A non-significant trend was also observed for the plant type (F= 2.425, p= 0.059). For quantitative traits, only a trend towards an effect of time since CA adoption was observed for the seed mass (F= 2.446, p= 0.065).

Table 2 near here

3.2.1 Raunkiær's life form

The first component of the Raunkiær's life form PCA biplot (Figure 1a) was associated with differences in ratio of phanerophytes to geophytes and explained 51.6% of the variance. The second component, explaining 38.5% of the variance, separated chamaephytes, therophytes and hemicryptophytes from phanerophytes and geophytes. The greatest link distance occurred between phanerophytes, geophytes and chamaephytes, indicating that the most relative variation occurred between these three attributes. The shortest link, indicating consistency in their ratio over communities, was found between therophytes and hemicryptophytes. By

interpreting the position of ellipses, we identified a higher ratio of chamaephytes, therophytes and hemicryptophytes vs phanerophytes and geophytes weeds for the age group 1 and a reverse trend for old fields in CA (age group > 10).

Fig 1 near here

3.2.2 Germination period

The first component of PCA biplot (58.1% of the variance) was associated with a difference in ratios between summer-germinated plants and all other plants (Figure 1b). The second component (25.2% of variance) was associated with the difference in ratios between spring-germinated plants and plants with germination mainly in fall to spring or spring to summer. These changes in ratios appeared to have little link with the time since the conversion. The fields that had been in CA for more than 10 years, had relatively more plants with summer germination than the other groups of fields.

3.2.3 Flowering period

The first component of PCA biplot (32.7%) discriminated between weed communities with higher ratio of plants with a summer flowering vs plants able to flower all year (Figure 1c). The second dimension (29.4%) was affiliated with the differences in ratios between spring and a group of attributes (summer to autumn, spring to summer, and spring to autumn). Communities of age group 1 showed a relatively higher proportion of plants capable of flowering all year round while the other age groups had higher proportions of summer flowering plants. Weed communities for age group >10 also appeared to have a relatively higher proportion of spring flowering plants.

3.2.4 Ellenberg's indicator value for light

The first component of the Ellenberg's indicator value for light biplot (Figure 1d) explained 41.8 % of the variance and was affiliated with the difference between the ratios of the score 5 and the score 6. The second component was affiliated with the difference in ratios of heliophile (7, 8, and 9) and shade-tolerant species (4 and 5). The second component explained 27.7 % of the variance. The strongest links were found between the score 4 and 5. Weed

communities of the age group 1 appeared to have less variability in the ratios of attributes than others age groups. More heliophilous weeds were linked to the age group 1, while proportions of shade-affiliated weeds (scores 4 and 5) were higher in the other age groups.

3.2.5 Plant type

Attribute ratios for the age groups 1 and 2-5 appeared to be more variables within the age groups in comparison with others age groups. The figure 2a also showed a trend to an increase of graminoids proportions during the first ten years of CA (age groups 2-5 and 6-10) and in the oldest systems (age group >10).

3.2.6 Seed mass

The CWM of the seed mass tended to increase continuously over the CA age groups (Figure 2b). Median values of the CWM seed mass increased from 2.62 mg in the age group 1 to 5.19 mg in the age group >10. Weed communities with very high CWM values (up to 20 mg) appeared for the age groups 6-10 and >10.

4 DISCUSSION

The results presented above on successfully established weeds (able to maintain and/or to reproduce) confirmed that not all functional responses of weed communities to the adoption of CA are visible during the first years of CA. Indeed, some functional shifts were spread over the 21-year age gradient of continuous application of CA.

Of all the traits included in this study, the specific leaf area and the leaf dry matter content were found to be the least influenced traits by the time since CA adoption. We expected an unfavourable filtering for species with high internal conductivity (high specific leaf area) and low investment in structural tissues (low leaf dry matter content), as it has been observed in field margins (Carlesi et al., 2013). Unlike others traits, these traits can be extremely variable within species (Kichenin et al., 2013). In this study, results suggested that the observed intraspecific variability would be mostly due to phenotypic plasticity. Using data from the database, we only captured the possible response of weed communities to CA

resulting from a change in composition, thus excluding an intraspecific adaptation in plant physiology. We can therefore conclude that the weed composition changes that may occur along the age gradient of CA, did not alter the capacity of plants to use resources or to compete. A similar result was found by Armengot et al., (2016) for specific leaf area in a no-till system. Although no change was observed for both traits, the results for seed mass could indicate a change in competitive ability at the early stage of weed development. It was expected that there would be a filtering towards smaller seeds, capable of natural seed burial, as it has been observed for reduced or no-tillage systems (Hernández Plaza et al., 2015; Armengot et al., 2016). On the contrary, our results showed an opposite trend, i.e an increase of the CWM value of seed mass with time since CA adoption. This increase of seed mass can correspond to a progressive shift toward smaller seeds with high colonizing capacity in early years of CA to larger seeds with high competition capacity in the oldest age groups, as observed in secondary succession on meadows (Zhang et al., 2018). The presence of permanent residue cover on the soil surface (cover crops or dead mulch) could have contributed to this shift by requiring additional resources for weed seeds to germinate (Teasdale, 1996), thus favouring weeds with larger seeds. The CWM values of this trait appeared quite variables, especially in the oldest systems (age groups 6-10 and >10), meaning that there were differences between communities, which could result from variations in weed management.

Regarding the mode of seed dispersion, we expected to find more wind-disseminated species in the youngest CA fields, which are typically rapid colonizers of undisturbed agroecosystems (Zanin et al., 1997; Young and Thorne, 2004). We also expected an increase of seed dispersion mechanisms dependents of others communities such as zoochory due to a better soil life activity in CA (Henneron et al., 2015). However, although anemochory and zoochory represented an important part of seed dispersion mechanisms of weed communities (19.9 and 30.8%, respectively), no change was observed with CA age. Since most farmer using CA in France use reduced tillage systems before adopting CA (Derrouch et al., 2020b) and because reduced tillage is also known to favour anemochore species (Swanton et al., 1993), we hypothesize that changes in seed dispersal mechanisms may have been masked by the legacy effects of past practices before adoption of CA. Some anemochorous and zoochorous species may have colonized the fields before the adoption of CA and persisted over time, as illustrated by the most frequent species in the dataset, i.e. *T. officinale*.

The lack of effect of the CA age on the soil seedbank longevity is consistent with results found by Armengot et al. (2016) on no-till systems. In agroecosystems, soil tillage has

a major influence on soil seedbank dynamics (Cordeau et al., 2017). By burying the seeds, soil tillage induces dormancy, thus lengthening seed persistence over time (Albrecht and Auerswald, 2009). Without tillage, most seeds remain localized near the soil surface (Clements et al., 1996), a condition deemed to be unfavourable to weed seed germination because of poor seed-soil contact et al.1984) but suitable for predation (Petit et al., 2017). Consequently, their persistence in the soil should decrease. The lack of change observed with time since CA adoption could result from an increase in soil life activity in CA fields (Henneron et al., 2015). By facilitating biological seed burial, macrofauna and megafauna may have replaced part of superficial tillage effect (Smith et al., 2005). In addition, the potential decrease in the longevity of soil seedbanks could have been masked by the fact that short-lived seeds are more rapidly affected by changes in filtering pressure than persistent seeds (Albrecht and Auerswald, 2009).

The effect of the maximum soil coverage on weed communities can also be observed through the changes identified in the Ellenberg's indicator value for light. In the first year after CA adoption, the weed communities appeared to be composed only of heliophile species (scores of 7, 8 and 9). By voluntarily decreasing the available light for weeds, farmers allowed colonizing species with an intermediate light affinity (Ellenberg's indicator value for light of 4, 5) to establish and reproduce in fields. Although the results showed an increase in weed species more tolerant to shade, the majority of the CA weeds community remained composed of heliophile weeds.

Regarding the Raunkiær's life forms, with the decrease in mechanical soil disturbances, an increase of all perennial life forms (Zanin et al., 1997; Trichard et al., 2013) was expected. Nevertheless, the proportions of hemicryptophytes and chamaephytes were higher in the age group 1. This observation could be the result of the progressive soil tillage reduction chosen by farmers before adopting CA (Derrouch et al., 2020b). Age groups 2-5 and 6-10 appeared as an intermediate state between the other groups, with higher proportions of geophytes and phanerophytes than age group 1 and higher proportions of therophytes, hemicryptophytes and chamaephytes than age group >10. Although the proportion of geophytes and phanerophytes increased with continuous application of CA, the proportion of therophytes in the weed communities in CA remains unaffected. Most of the common (*A. myosuroides*, *C. album*) and abundant species (*V. hederifolia*, *D. sanguinalis*, *S. pumila*, *A. hybridus*) were therefore therophyte species.

The results showed a tendency toward an increase of graminoids with CA age. Weed communities in the age groups 6-10 and >10 appeared to be less variables in their proportions

of eudicotyledons/ graminoids and composed of a higher proportion of graminoids. This trend has already been observed in systems with reduced tillage (Murphy et al., 2006) or in CA (Trichard et al., 2013) and may result from a smaller range of chemical solutions that can be used on grasses on wheat crop.

Both the germination and flowering periods were affected by the time since CA adoption. The age groups 2-5, 6-10 and >10 had a higher proportion of summer flowering than the age group 1 and the oldest age group (> 10) showed a higher proportion of species germinating in summer. This filtering towards summer life span weeds in CA could be due to the opportunity for weeds to establish during the intercropping period. In CA, due to the absence of post-harvest disturbance by tillage and to the use of chemical weeding mainly before the sowing of the next crop, the intercropping period represents a new temporal niche for weeds. In addition, these changes could have been facilitated by the third principle of CA, the crop diversification. This crop diversification, applied by half of farmers when adopting CA (Derrouch et al., 2020a) is generally optimized by farmers after the first five years of CA to achieve sustainable weed management (Derrouch et al., 2020a). The introduction of spring and summer crops during the post-adoption period, could explain the observed increase in summer germination proportions in the age group >10. Thus, in a wheat crop (from late winter to intercropping period), summer weeds (*C. album*, *D. sanguinalis*, *S. pumila*, *A. hybridus*) generally more affiliated to summer crops such as maize (*Zea mays* L.) or soybean (*Glycine max* (L.*)* Merr.) have the opportunity to develop and reproduce.

5 Conclusions

The objective of this study was to identify functional shifts in weed communities over a 21-year age gradient since CA adoption. Results showed that functional shifts observed in fields recently converted to CA (two to five years) remain visible in the older ones. This was particularly the case for shifts towards more phanerophyte and geophyte life forms, graminoids, weeds with larger seeds, spring- to summer- germinating and summer-flowering species. Nevertheless, some functional shifts occurred later, i.e. ten year after CA adoption, such as an increase of summer-germinating and spring-flowering weeds. As changes in weed community functional composition could potentially worsen current weed management efficacy, this work could therefore provide knowledge to CA farmers and farmers moving towards CA to redesign the weed management tactic according to expected weed community evolution.

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CONFLICT OF INTEREST

The authors reported no potential conflict of interest.

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Figure legends

FIGURE 1: Response traits significantly affected by time since CA adoption. In composition data PCA biplot (a, b, c and d), the relevant variables are represented by the links (*i.e*. the difference between two arrowheads) which correspond to the distance of log ratio between two components.

FIGURE 2: Trend observed with time since CA adoption. Because only two attributes composed the trait "plant type", the distances of log ratio were represented with a boxplot (a). For the quantitative trait "seed mass", the CWM values were represented using a boxplot (b)

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616 **TABLE 1** Mean community weighted mean (CWM) value or percentage of attributes

Categorical traits	Attribute	Number of species	Geometric mean (and standard deviation) in %*
Raunkiaer's life form	Therophyte	98	71.2 (± 20.1) %
	Hemicryptophyte	88	23.1 (± 18.2) %
	Geophyte	15	3.7 (± 6.1) %
	Chamaephyte	5	0.03 (± 0.2) %
	Phanerophytes	20	1.97 (± 3.8) %
Soil seedbank longevity	Transient	123	35.8 (± 22.8) %
	Transient to short term	29	15.9 (± 18.1) %
	Short term persistent	15	18.5 (± 22.8) %
	Transient to long term	34	15.7 (± 14.6) %
	Short term to long term	13	9.5 (± 14.2) %
	Long term persistent	12	4.5 (± 11.8) %
Plant type	Eudicotyledon	193	73.2 (± 24.7) %
	Graminoids	33	26.8 (± 24.7) %
Flowering period	All year	4	2.99 (± 6.5) %
	Spring	13	1.7 (± 3.4) %
	Spring to summer	48	28.7 (± 24.4) %
	Spring to autumn	53	20.4 (± 17.5) %
	Summer	22	4.3 (± 8.6) %
	Summer to autumn	86	42 (± 24.1) %
Germination period	All year	58	23.6 (± 17.7) %
	Spring	52	7.5 (± 10.3) %
	Spring to summer	34	23.3 (± 18) %
	Summer	14	10.8 (± 21.2) %
	Autumn to spring	68	34.8 (± 25.5) %
Mechanism of seed dispersal	No mechanism	73	46.9 (± 22.8) %
	Anemochory	62	19.9 (± 14.7) %
	Zoochory	83	30.8 (± 22.9) %
	Autochory	8	2.35 (± 7.9) %
Ellenberg's indicator value for light	Shadow species - 4	2	1.9(± 6.9) %
	5	13	2.4 (± 4.8) %
	6	16	6.9 (± 9.7) %
	7	102	50.3 (± 23) %
	8	87	38.4 (± 23.9) %
	Full light species - 9	6	0.1 (± 0.7) %
Quantitative traits	**Unit**	**Mean CWM attribute (± standard deviation) on the 100 fields***	
Seed mass	mg	4.9 (± 3.9)	
Specific leaf area	$mm^2.mg^{-1}$	25.4 (± 3.2)	
Leaf dry matter content	$mg.g^{-1}$	187.2 (± 26.3)	

*After imputation of zero counts, see materials and methods section for the detailed method

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TABLE 2 Effect of the time since adoption of Conservation Agriculture (CA) on the ten traits. Values of permutational test using distance matrices (PERMANOVA) with the ten traits as responses variables and time since CA adoption as explanatory variable (4 classes of group age). In bold, significant results ($p < 0.05$).

Response traits	Time since CA adoption		
	R^2	F	p
Categorical traits			
Raunkiær's life form	0.113	4.06	**0.001**
Soil seedbank longevity	0.048	1.641	0.092
Plant type	0.070	2.425	0.059
Time of flowering	0.097	3.422	**0.001**
Time of germination	0.078	2.719	**0.013**
Seed dispersal	0.024	0.781	0.614
Ellenberg's indicator value for light	0.088	3.105	**0.002**
Quantitative traits			
Seed mass	0.071	2.446	0.065
Specific leaf area	0.015	0.4997	0.681
Leaf dry matter content	0.005	0.148	0.927

FIGURE 1

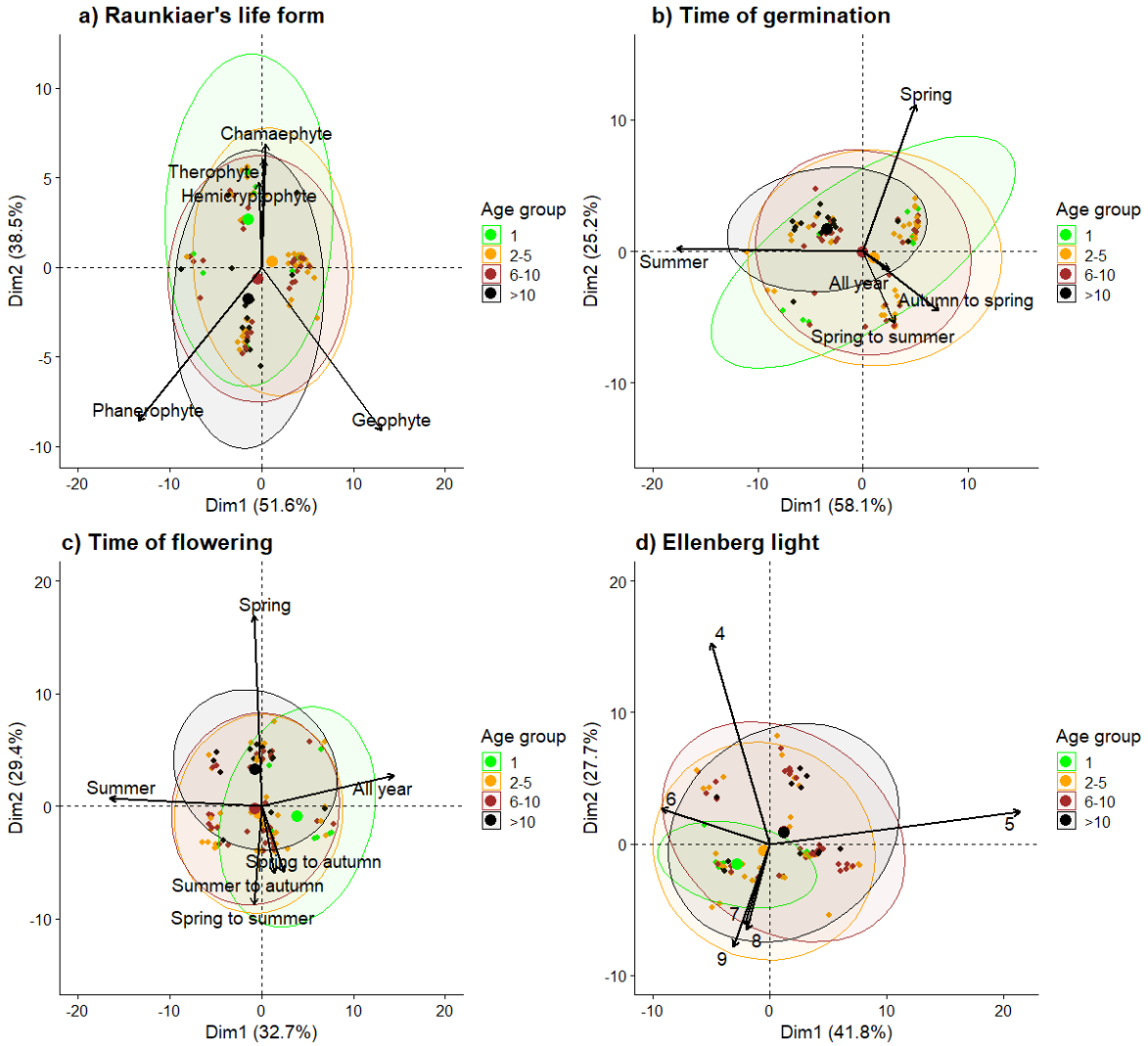
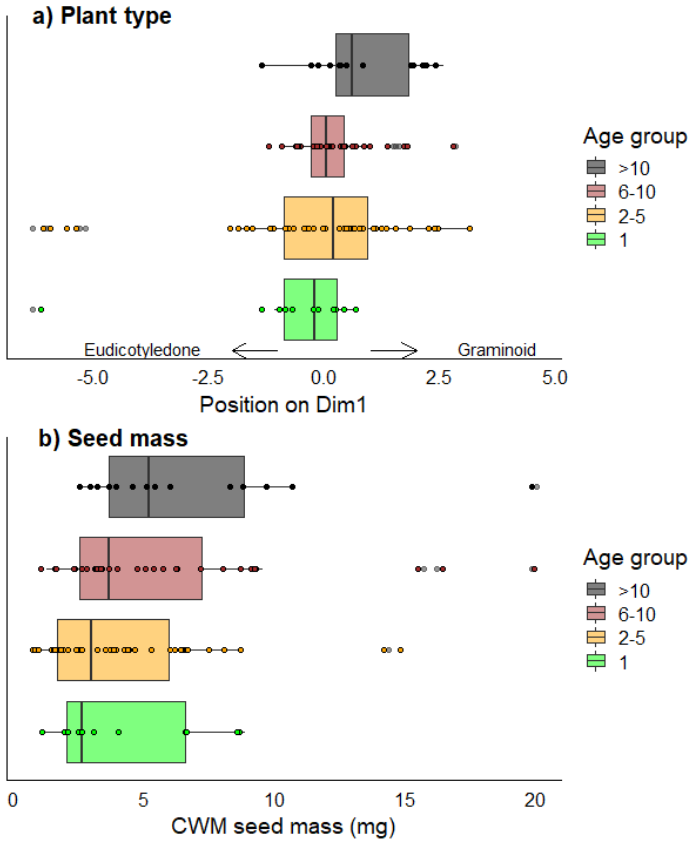

a) Raunkiaer's life form
Chamaephyte
Therophyte
Hemicryptophyte
Phanerophyte
Geophyte
Dim2 (38.5%)
Dim1 (51.6%)
Age group
1
2-5
6-10
>10
b) Time of germination
Spring
Summer
All year
Autumn to spring
Spring to summer
Dim2 (25.2%)
Dim1 (58.1%)
c) Time of flowering
Spring
Summer
All year
Spring to autumn
Summer to autumn
Spring to summer
Dim2 (29.4%)
Dim1 (32.7%)
d) Ellenberg light
4
5
6
7
8
9
Dim2 (27.7%)
Dim1 (41.8%)

FIGURE 2


a) Plant type
Age group
>10
6-10
2-5
1
Eudicotyledone
Graminoid
-5.0
-2.5
0.0
2.5
5.0
Position on Dim1
b) Seed mass
Age group
>10
6-10
2-5
1
0
5
10
15
20
CWM seed mass (mg)