Field Crops Research 289 (2022) 108724

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Conservation agriculture practices lead to diverse weed communities and higher maize grain yield in Southern Africa

Blessing Mhlanga [a,*], Laura Ercoli [a], Christian Thierfelder [b], Elisa Pellegrino [a,*]

[a] Scuola Superiore Sant'Anna, Institute of Life Sciences - BioLabs, Pisa, Italy
[b] International Maize & Wheat Improvement Centre (CIMMYT), Southern Africa Regional Office (SARO), Harare, Zimbabwe

ARTICLE INFO

Keywords:
Conservation agriculture
Weed community
Weed community diversity
Grain yield, Weed density

ABSTRACT

Weed development is one of the major constraints to cereal cropping systems in Southern Africa with potential severe crop losses. Understanding weed community responses to different conservation agriculture (CA) components (*i.e.*, no-tillage, NT; crop rotation, R; and mulching, M) and/or their combinations is crucial in Southern Africa where farmers apply different combinations depending on local context. Here, for the first time, we assessed how weed density, community diversity and structure respond to different combinations of CA components [conventional tillage (CT), CT+M, CT+R, CT+M+R, NT, NT+M, NT+R, NT+M+R]. The study was carried out over three seasons at two locations with contrasting soil textures *i.e.*, clayish, and sandy. At the sandy location, across seasons, weed density (number of individuals per unit area) and community diversity (distribution of individuals within the species) were significantly and positively affected by precipitation and not by cropping system. Weed richness (number of species) was affected by the interaction of season and cropping system, with the highest number of weed species being recorded in the NT+M+R system in the seasons with medium to high precipitation. At the clayish location, an opposite pattern was observed, and weed density was lower in seasons with medium-high precipitation than under low precipitation. Weed community diversity was 50 % higher under NT+M than under CT+R, whereas weed species richness decreased with the increase of precipitation. At both locations, the implementation of rotation and mulching either in NT or CT systems resulted in the modification of the structure of weed community with respect to CT and NT alone, and these CA combinations were associated with highest maize grain yield. Overall, eight weed species common to both locations were responsible for most of the community structure differences among cropping systems. Structural equation modelling showed that at the sandy location precipitation did not affect grain yield, but positively affected weed density, diversity, evenness, and richness. By contrast, at the clay location, precipitation positively affected grain yield, but did not modify weed density and evenness, and reduced weed community diversity and richness. At this location, weed density negatively affected grain yield. The differential weed-crop relationship supports the need to find a site-specific equilibrium between the control of weeds and the maintenance of their diversity.

1. Introduction

Weed control is one of the major constraints to cereal crop production in Sub-Saharan Africa (SSA), having a potential cereal crop loss of up to 34 % (Oerke, 2006; Tittonell and Giller, 2013). Weed control is hindered by shortage of manpower which results in late management of weeds and other activities in general, thus leading to higher crop-weed competition for nutrients, water, light, and space (Dahlin and Rusinamhodzi, 2019). The yield outcome of smallholder farmers with small landholding sizes and commonly cultivating cereals, such as maize (*Zea mays* L.) and sorghum [*Sorghum bicolor* (L.) Moench] as monocrops, can thus be largely affected by changes in weed management practices. Such practices include early weeding, soil fertility zoning in nutrient management, rotation, intercropping, legume diversification, mulching (Silberg et al., 2019).

Smallholder farmers rely on manual control of weeds using hand hoes and this is a tedious and labour intensive activity during the cropping cycle (Nyamangara et al., 2014). Further, smallholders are often situated in soils of poorer fertility due to previous soil erosion and unsustainable management, which leads to an increase in parasitic

---

* Corresponding authors.
E-mail addresses: b.mhlanga@santannapisa.it (B. Mhlanga), e.pellegrino@santannapisa.it (E. Pellegrino).

https://doi.org/10.1016/j.fcr.2022.108724
Received 9 March 2022; Received in revised form 4 October 2022; Accepted 10 October 2022

weeds, such as the witch weed (*Striga* spp. Lour.) (Ekeleme et al., 2014). Such weeds are difficult to control due to their means of propagation and can also lead to total yield losses if not controlled in time (Rodenburg et al., 2016).

Despite their negative effects on crop growth, weed diversity can provide a range of agroecosystem services promoting crop production and environmental protection (MacLaren et al., 2020; El Omari and El Ghachtouli, 2021). Indeed, rather than eradicate weeds, different options are suggested that aim at regulating populations to limit their negative impacts, while conserving diversity and functionality. A more diverse weed community was shown to increase crop health, diversity and contribution of bees to crop yields (Bretagnolle and Gaba, 2015), and to be less competitive with any given crop depending on the species present (*e.g.*, Storkey and Neve, 2018; Ferrero et al., 2017). Recently, it was found at four critical growth stages of winter cereals, that increased weed diversity better explains the reduction of yield loss than decreased weed density (Adeux et al., 2019).

Conservation agriculture (CA) which is based on the implementation of the principles of minimum soil disturbance, crop diversification, and permanent soil cover with organic material, has been promoted as a more sustainable crop production system that maintains or enhances yields, while improving soil health and reducing soil degradation (FAO, 2019). The implementation of the components of CA, such as mulching and crop diversification, has been already shown to control parasitic weeds, such as *Striga hemonthica* (Del.) Benth. (Rodenburg et al., 2020). Crop diversification with vigorously growing legumes increases competition with weeds for water, nutrients, and light, and thus reduces their growth (Sharma et al., 2021). However, the management of weeds under CA especially during the early years of conversion has been identified as the main constraint to its adoption (Nichols et al., 2015) and requires additional good agriculture practices (Thierfelder et al., 2018). Weed pressure could be a factor contributing to failure in conventional to no-tillage conversion, in the short and medium terms (Swanton et al., 1993). Indeed, under no-tillage (NT), most weed seeds are exposed on the soil surface where conditions are conducive for germination and hence this leads to high weed densities (Baker et al., 2018). If weeds are allowed to flower and shed seeds, new seeds are added to the seed bank. However, under conventional tillage (CT) no new weed seeds are ploughed to the surface and this could lead to a depleted weed seed bank over time (Muoni et al., 2014).

Since the implementation of different CA components likely results in variable weed community responses, and smallholder farmers tend to practice them in different combinations, it is important to study the implementation of these different combinations on weed community diversity and structure. Such knowledge is still lacking and is crucial for understanding and practicing weed management under CA, especially in the context of Southern Africa. In a recent review, it was highlighted that no single solution can solve all weed control challenges under current CA agricultural systems (Lee and Thierfelder, 2017; Kodzwa et al., 2020). Conflicting findings were reported on the effect of tillage on weed pressure, as no-tillage did not modify weed biomass compared to CT in dry environments, while in more humid environments CT better controlled weeds (Ngwira et al., 2014). Rotation of maize with some cover crops such as velvet bean (*Mucuna pruriens* (L.) DC) reduced weed number and dominance of problematic weeds over time, while with others (*e.g.* black sunnhemp, *Crotalaria juncea* L. and cowpea, *Vigna unguiculata* Walp) maize rotations were associated with high weed densities (Mhlanga et al., 2015). Finally, mulching that is affected by crop identity and rotation (Ercoli et al., 2017) was reported to be highly effective in weed control across diversified environments, but the effect is variable depending on the amount of crop residues (Teasdale and Mohler, 2000; Ngwira et al., 2014). A general linear increase in residue biomass results in an exponential decay in the percentage of germinated weed seeds that successfully emerge, although the exact relationship depends heavily on residue characteristics. Therefore, it is important to assess the response of weed communities to the interactive effects of CA components. There is only one recent study by Fonteyne et al. (2020) who assessed in Mexico the effects of the different combinations of CA components after 13 years with and without herbicide application on weed biomass, density, and diversity. While no significant differences were observed in weed density across CA combinations with and without herbicide application; with herbicides, a significant reduction of weed biomass per crop (wheat and maize) was observed under crop rotation, as well as under NT in wheat. Irrespective of herbicide applications, perennial weeds were lower under NT and rotation, while rotation promoted weed diversity, which may have helped the crops avoid weed problems. However, in the context of Southern Africa, herbicide use is limited by different factors, such as their cost and availability, and thus, farmers rely mainly on manual hoe weeding (Lee and Thierfelder, 2017). Moreover, crop diversification by Fonteyne et al. (2020) was accomplished through rotation of two cereals, maize and wheat, and such a sequence is not commonly cultivated by the smallholder farmers in Southern Africa that usually integrate legumes, such as groundnut (*Arachis hypogea* L.) and cowpea (*Vigna unguiculata* L.) in cereal-based systems (Franke et al., 2018). Thus, in the present study, we aimed to assess in the early years (medium-term: after six seasons), weed community responses to the different combinations of CA components, with weed control mainly based on hand hoe weeding and on the integration of a vigorously growing legume crop, such as cowpea, as a rotational crop. Accordingly, the conditions of the experiments in our study reflected the situation of the smallholder farmers in Southern Africa (*e.g.*, soil texture: sandy and clay sites).

We therefore hypothesised that the implementation of all the three CA components leads to: (i) a reduction in weed density; and (ii) an increased weed community diversity positively affecting or not compromising crop yield. We also aimed to dissect the potential seasonal effects on weed density and community diversity using seasonal precipitation. The elucidation of these topics is necessary to set-up optimal weed control strategies with the goal of looking for an equilibrium between the control of damage caused by weeds and the conservation of biodiversity and ecosystem functioning.

2. Material and methods

2.1. Experimental field locations

The study was carried at two locations with contrasting soil textures: Domboshawa Training Centre (DTC) (latitude 17.62°S; longitude 31.17°E; and altitude of 1560 m above sea level) and University of Zimbabwe (UZ) (latitude 17.73°S; longitude 31.02°E; and altitude of 1503 m above sea level). The soil at DTC has clay, sand, and silt contents of 220 g kg^{-1}, 730 g kg^{-1}, and 50 g kg^{-1}, respectively, is characterized by a sandy clay loam texture (further referred to as sandy location) (Soil Survey Staff, 1975), classified as *Arenosols* (IUSS Working Group WRB, 2015), and has an organic carbon content (SOC) of 7.3 g kg^{-1}. The soil at UZ has clay, sand, and silt contents of 400 g kg^{-1}, 390 g kg^{-1}, and 210 g kg^{-1}, respectively, is characterized by a clay texture (further referred to as clay location) (Soil Survey Staff, 1975), classified as *Rhodic Lixisols* (IUSS Working Group WRB, 2015), and has a SOC content of 16.8 g kg^{-1}. The experiments at the two locations started in the summer crop growing season of 2013, and in this study, we reported data collected in the 2019, 2020, and 2021 growing seasons. According to the Köppen-Geiger climate classification, the climate of the sites is classified as warm temperate with dry winters and hot summers (Kottek et al., 2006). At DTC, the 2021 season had the highest cumulative rainfall of 932 mm, while the 2020 season had the lowest cumulative rainfall of 471 mm [coefficient of variation (CV) = 35.5 %] (Fig. S1a). During the three growing seasons at UZ, there was an increase in cumulative rainfall from 2019 to 2021, and the highest rainfall was observed in 2021 (699 mm; CV = 29.9 %) (Fig. S1). Average maximum seasonal temperatures were highest in the 2021 season, reaching 29.2 °C at DTC and 29.9 °C at UZ. Both locations experienced mid-season dry spells in all the seasons

(Fig. S1). Weather data was recorded using weather stations that were located about 5 m from the experimental site.

2.2. Experimental set-up and crop management

The experiments were set up in a randomised complete block design (RCBD) with eight treatments (referred to as cropping system hereafter) replicated four times (Table S1, Fig. S2):

i. Conventional tillage (CT)
ii. Conventional tillage plus mulching (CT+M)
iii. Conventional tillage plus rotation (CT+R)
iv. Conventional tillage plus mulching and rotation (CT+M+R)
v. No-tillage (NT)
vi. No-tillage plus mulching (NT+M)
vii. No-tillage plus rotation (NT+R)
viii. No-tillage plus mulching and rotation (NT+M+R); referred to as CA herein

For the treatments based on CT, land preparation was done through digging with a hand hoe to simulate ploughing and crops were sown in riplines that were created afterwards using an animal-drawn Magoye ripper at DTC, and in basins created with a hand hoe at UZ. For the NT-based treatments, crops were sown in riplines that were created using an animal-drawn Magoye ripper at DTC, and in basins created with a hand hoe at UZ. For treatments involving rotation, plots were split into half and maize was sown in a one-year rotation with cowpea (with phases of the rotation present in each year) while for monocropping treatments, sole maize was sown. For treatments that involved mulching, crop residues were retained on the soil surface at a precisely weighed rate of 2.5 t ha^{-1} at all locations, while for those with no mulching, residues were removed at harvest. For plots in which mulch was not adequate to reach the required rate, maize residue was imported from adjacent maize fields managed under the same conditions. The rate of mulch was determined based on the average rate of mulch that local smallholder farmers can apply due to the competition for maize residue for ground cover and fodder for livestock.

The treatments were established in plots measuring 12 m × 6 m (72 m^2). Maize was sown at an interrow spacing of 90 cm and an intra-row spacing of 25 cm, and cowpea at an interrow spacing of 45 cm and an intra-row spacing of 25 cm to achieve plant populations of 44,444 and 88,888 plants ha^{-1}, respectively. At sowing, both maize and cowpea received a basal fertiliser at the rate of 11.6 kg N ha^{-1}, 10.1 kg P ha^{-1}, 9.6 kg K ha^{-1}, and maize further received a top-dressing fertiliser in the form of ammonium nitrate (NH_4NO_3) at the rate of 46 kg N ha^{-1}, split applied four and seven weeks after planting. At the beginning of the season, weeds were controlled by spraying glyphosate [*N*-(phosphonomethyl) glycine], at the rate of 1.025 g active ingredient ha^{-1} using a knapsack sprayer. The glyphosate was sprayed overhead all existing living weeds. This was followed by manual hoe weeding whenever weeds were 10 cm tall or 10 cm in diameter for stoloniferous weeds and weeds were left on the soil surface. This meant that weeding was done twice at approximately 30 and 60 days after sowing crops (DASC) since it corresponding to the periods when weeds had reached 10 cm height or diameter. The use of hand hoes for weeding during the cropping season is a common practice by smallholder farmers in the region. Diseases and pests were chemically controlled whenever necessary.

2.3. Maize yield, weed density, species counts and community diversity

For grain yield assessment, all maize plants found within a net plot area of 18 m^2 (5 m × 3.6 m) were harvested from each plot and the weight recorded (gross plot weight). Maize cobs were removed from the stalks and a subsample of 10 cobs per plot was weighed for fresh weight, air-dried for four weeks, and weighed again for dry weight. The subsampling of cobs was necessary as this reduced the bulkiness of the sample net plot sample which had to be transferred from the experimental field for air-drying. Grain moisture content was determined, and yield was expressed at 12.5 % moisture content based on the gross plot weight and the corrected weight from the sub-samples. Maize stover for the gross plot was weighed for all plants. A subsample of about 500 g was taken for each plot and this was air-dried until a constant weight and reweighed and plot stover was determined on a dry weight basis using the gross plot weight and the moisture-corrected weight of the subsample. Yield data were calculated per unit of surface area (ha).

The number of weed species and their abundances (number of individuals per species) were collected from quadrats that measured 0.5 m × 0.5 m placed randomly four times in each plot before each weeding which correspond to the cob development stage (V8) and the pollination stage (R1). However, weed counts were pooled across sampling times to assess the appearance of the weeds over the whole season. Quadrats were placed in the row spacing avoiding the outer boarder rows. All weeds within each quadrat were identified to species level and classified as dicots and monocots, and perennials and annuals based on their morphology and life cycle, respectively, using the guidelines in Makanganise and Mabasa (1999) and Botha (2010). Since each stem has the potential to propagate into a new plant for perennial monocots, stem counts were done instead of plant counts. Data from the quadrats were used to determine weed density (number of individual weeds within the four quadrats expressed to m^{-2}), weed species density (number of individual weeds per species within the four quadrats expressed to m^{-2}), and to determine weed community diversity, evenness, and taxonomic richness (number of species).

2.4. Calculations and statistical analyses

2.4.1. Weed community diversity

All analyses were done separately for each location. Weed community diversity was computed using Shannon's diversity (*H'*), Pielou's evenness (*J'*), and Margalef's richness (D_{mg}) indices as suggested by Magurran (2004). Shannon-Weiner index (Shannon's *H'*) (Shannon and Weaver, 1949) was calculated as follows:

$$H' = -\sum_{i=1}^{S} P_i(In \quad P_i)$$

where *H'* is the Shannon-Weiner diversity index, p_i is the proportion of individuals belonging to the i^{th} species and *S* is the total number of species. Shannon's diversity describes the distribution of individuals within the species retrieved in the samples. Thus, we can have high number of species with a low Shannon's diversity index if most individuals belong to few species or with a high Shannon's diversity index if individuals are equally distributed within all species.

Pielou's evenness index (Pielou, 1969) was calculated as the ratio of observed diversity to maximum diversity as follows:

$$J' = H'/H_{max} = H'/lnS$$

where *H'* is the Shannon's diversity, and H_{max} or *lnS* is the maximum Shannon diversity in which all present species appear in equal abundances for a community, and *S* is the number of observed species. Evenness compares the weed diversity among cropping systems and over time for each location and its values range between 0 and 1, representing an absolute dominance and equal species abundance, respectively.

The Margalef's species richness (Margalef, 1972) aims at compensating for sampling effect by dividing the number of species recorded, *S*, by the number of individuals, *N* (plants m^{-2}), in the sample using the following formula:

$$D_{mg} = \frac{S-1}{lnN}$$

Specifically, Margalef's richness estimates the total number of species within a sample.

Dominance of weeds was assessed based on recurrence index percentage (RI %) which was determined as the number of quadrats in which a species appeared over the total number of quadrats sampled at each location in each season (Mahgoub, 2019). Based on the RI %, weeds were grouped into two classes of constancy ranges *i.e.*, 1–25 %, and > 25 %. To assess the effects of cropping systems and seasons on individual weed species densities, only weeds that exhibited > 25 % constancy in all seasons were considered. These weeds were *Amaranthus hybridus* L. (AMACH), *Bidens pilosa* L. (BIDPI), *Commelina benghalensis* L. (COMBE), *Galinsoga parviflora* Cav. (GASPA), and *Richardia scabra* L. (RCHSC) at DTC; and BIDPI, GASPA, *Ipomoea purpurea* (L.) Roth (PHBPU), *Leucas martinicensis* (Jacq.) R. Br (LEUMAR), and RCHSC at UZ.

All weed data were assessed for normality and where necessary, data were fourth-root-transformed before further analyses. Effects of cropping systems, seasons and their interaction (treated as fixed factors) on total weed density, weed species abundance, and diversity indices (H', J', and D_{mg}) were assessed using linear mixed models using the 'lme4' package (Bates et al., 2015) in R environment (R Core Team, 2022). In the analyses, replicates were included in the models as random factors. Means of back-transformed data were reported. Significance of fixed effects was tested using F-tests and where means were significantly different, they were contrasted using a mean comparison procedure following Tukey tests ($P < 0.05$) in 'emmeans' package (Lenth, 2019) in R environment.

2.4.2. Weed community structure

To analyse the effect of seasons, cropping systems, and their interaction on weed community structure, we used type III permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a semiparametric multivariate test which is similar to multivariate analysis of variance but generates pseudo-F ratios and P-values using the Monte Carlo permutation P(MC) test through resampling (999 permutations for our analysis) the resemblance measures. Thus, it is less sensitive to the assumptions of parametric tests which are usually infringed by community data (Anderson, 2001).

Weed species relative abundances (calculated as a proportion of all species) were fourth-root transformed so that the multivariate analyses would draw on all species instead of being dominated by a few species of high abundance or influenced by the rarer ones (Clarke et al., 2014a; b). Before the PERMANOVA, a resemblance matrix was constructed based on the Bray Curtis dissimilarity index (Bray and Curtis, 1957) as follows:

$$Bray - Curtis \quad (BC_{jk}) = \frac{\sum_{i=1}^{S} 2a_{ij} - a_{ik}}{\sum_{i=1}^{S} a_{ij} + \sum_{i=1}^{s} a_{ik}}$$

where BC_{jk} is the dissimilarity between samples j and k; a_{ij} and a_{ik} are the relative species abundance of species i in samples j and k, respectively, and S is the combined total density of the species in both communities. For factors that showed significances [P(MC) < 0.05 in PERMANOVA tests], comparisons were made within each significant factor level. Where group differences in community structure were detected, similarity percentage analysis (SIMPER) was done to detect the species responsible for the differences by calculating the percentage contribution of the species to the total effects and this was done at 100 %. Further, we carried out a permutation test for homogeneity of multivariate dispersions (PERMDISP) on each significant factor level. This test is used as a measure of multivariate beta diversity to check whether the significant group differences observed in PERMANOVA were also not influenced by differences in dispersion of group objects from the group centroid (alpha diversity).

Principal coordinates analysis (PCoA) was then performed to visualise relevant patterns in the data. All the multivariate analyses were performed using Primer 7 with PERMANOVA+ software (Clarke et al., 2014a; Anderson et al., 2008).

2.4.3. Effect of seasonal precipitation on weed density and community diversity

To explain the observed seasonal effects on weed density, H', J', and D_{mg}, we carried out linear regression analysis with seasonal precipitation as the predictor variable. Further, we assessed the effect pathway of precipitation on weed parameters (H', J', and D_{mg}) and maize grain yield using piecewise structural equation modelling (SEM) based on multiple regression using the 'piecewiseSEM' and package in R (Lefcheck, 2016). Models were fit using linear models and variables were standardised for the effects to be directly comparable and for each pathway, a standardized coefficient (λ) was estimated. In the models, we also calculated the covariance of H' and J'; H' and D_{mg}; and J' and D_{mg}. Final model fits were estimated by the Fisher's C test.

3. Results

3.1. Overall occurrence of weeds

Over the seasons of assessment, 30 weed species were observed across both locations in the plots and of these, 74 % were broadleaved dicotyledonous species, while the remaining were monocotyledonous grasses and sedges (Table S2). For both dicots and monocots, annual species were dominant, constituting 72 % and 75 % of the observed species at the sites, respectively. However, the occurrence of most of these species depended on the location and the season. For example, species, such as *Rottiboellia conchichinensis* (Lour.) W.D. Clayton (ROOEX), and *Euphorbia heterophylla* L. (EPHHL) only appeared at the clay location (UZ), while species, such as *Acanthospermum hispidum* D.C. (ACNHI) and *Galium aparine* L. (GALAP), only appeared at the sandy location (DTC), although sporadically. Some weeds, such as BIDPI, GASPA, and RCHSC, exhibited high occurrence, and they appeared in at least 25 % of the plots in most of the seasons at both locations. Annual dicots, such as PHBPU (L.) Roth (I), LEVMA, and *Sida alba* (SIDBA) exhibited dominance only at the UZ (clay location). At DTC (sandy location), dominance was exhibited by both annual dicots and perennial monocots, and these were AMACH, BIDPI, and COMBE (Table S2).

3.2. Effect of season and cropping system on weed density, individual species density, and community diversity

At the sandy location (DTC), there were significant seasonal differences in weed density and H', while Margalef's species richness (D_{mg}) was significantly affected by the interaction of season and cropping system (Table 1). Weed density and H' showed a similar trend in response to the inter-seasonal precipitation variation, and in 2020 when the precipitation was the lowest (Fig. S1a) both traits resulted in the lowest values (Fig. S3a, c). Thus, it is evident from the linear regressions that at DTC seasonal precipitation had a very strong positive and significant influence on weed density (Adj $R^2 = 0.86$), and a significant, but less strong positive influence on H' (Adj $R^2 = 0.28$) (Fig. S3b, d). Moreover, while weed species richness (D_{mg}) did not change among cropping systems in 2019 and 2021 (*i.e.*, medium, and highest precipitations), it was generally higher than in 2020 (*i.e.*, lowest precipitation). However, D_{mg} differences among treatments were small, ranging from 6.3 to 8.6 in (Fig. 1). Interestingly, the NT+M system showed a higher number of weed species (7.3)in comparison with the other systems in 2020 (on average 6.7), and the value was similar to the richness observed in all the systems in 2019 and 2021 (Fig. 1a). At the clay location (UZ), the interaction of season and cropping system significantly affected weed density (Table 1). Overall, in 2020 and 2021 (*i.e.*, medium and.

largest precipitations) cropping systems showed values significantly lower than those reported in 2019, the season with the lowest

Table 1

Effect of season and cropping system (System) on weed density, Shannon diversity (*H*'), Pielou evenness (*J*'), Margalef richness (*Dmg*), maize grain yield, and maize stover at Domboshawa Training Centre (DTC; sandy location) and University of Zimbabwe (UZ; clay location). *F*-values and degrees of freedom (DF) were derived from linear mixed effect models.

Location	Source	DF	Weed density[†]	*H*'	*J*'	D_{mg}	Maize grain yield	Maize stover
DTC	Season[‡]	2	147.8***	27.9***	2.7	137.1***	6.0**	6.3**
	System[‡]	7	1.1	0.5	0.8	1.2	2.7*	3.7**
	Season × System	14	1	1.3	1	1.9*	1.6	1
UZ	Season	2	4.7*	2.6	1.7	44.0***	71.6***	114.4***
	System	7	4.5***	2.3*	1.4	1.9	10.3***	13.5***
	Season × System	14	2.8**	1.5	1.4	1	1.5	1.8

[†] *F*-values with asterisks were significantly different: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$; [‡] Three seasons and eight cropping systems (see Table S1).

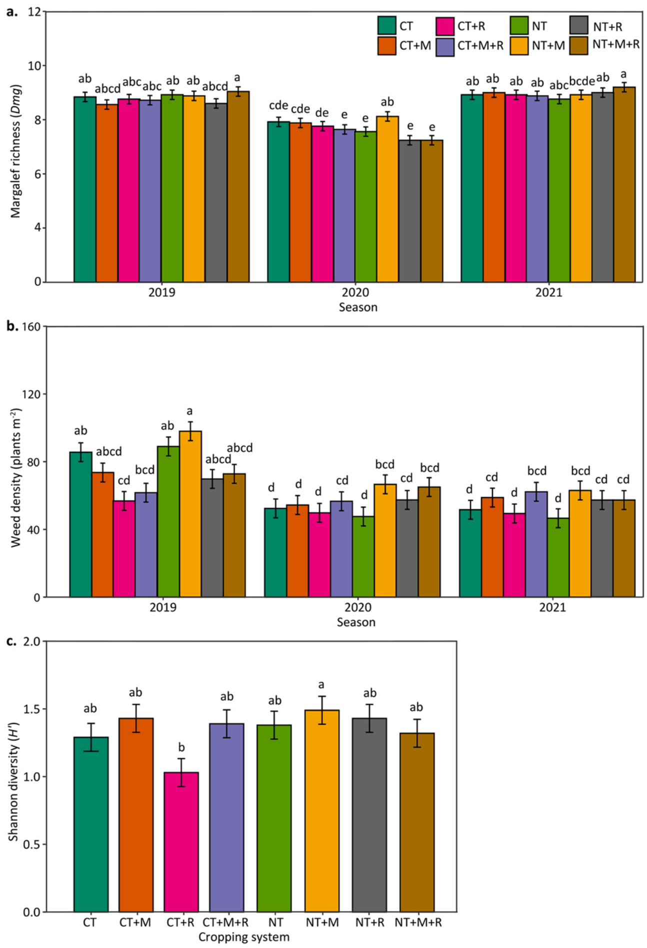

Fig. 1. Interaction between season and cropping system on Margalef richness (*Dmg*) at Domboshawa Training Centre (DTC; sandy location) (a); interaction of season and cropping system on weed density (cumulated over two sampling periods) at University of Zimbabwe (UZ: clay site) (b); effect of cropping system on Shannon diversity index (*H*') at UZ (c). Abbreviations of the cropping systems are: CT, conventional tillage; CT+M, CT plus mulching; CT+R, CT plus crop rotation; CT+M+R, CT plus mulching and rotation; NT, no-tillage; NT+M, NT plus mulching; NT+R, NT plus rotation; NT+M+R, NT plus mulching and rotation. Values are means ± SE of four replicates for each cropping system per season. Columns with different letters are significantly different from each other based on *P*-values reported in Table 1.

precipitation (2019) (Fig. 1b). Moreover, in the 2019 season, the NT+M system showed the highest weed density as compared to other cropping systems in 2020 and 2021 (Fig. 1b). The *H*' differed only among the cropping systems (Table 1) with the NT+M exhibiting the highest diversity of 1.5, while the CT+R showed the lowest diversity of 1.0 (Fig. 1c). D_{mg} significantly differed among the seasons (Table 1) with progressive but small decreases from 2019 to 2021 (from 8.7 to 8.1 and 7.8), thus, from the season with low precipitation (2019) to the seasons with higher precipitation (2021) (Fig. S3e, f). This was also confirmed by the significant, but negative good relationship (Adj $R^2 = 0.54$) between seasonal precipitation and D_{mg} (Fig. S3f). Finally, Pielou's evenness (*J*') did not differ among seasons and cropping systems at both locations.

For the weed species that exhibited dominance throughout the seasons at the sandy location (DTC) (Table S2), densities of all species were affected by seasonal differences (Fig. S4a–e), while those of BIDPI, GASPA, and RCHSC were also affected by cropping system (Table S3). However, interannual differences were more important as compared to cropping system effect (Fig. S4b, d, e, Table S3). As also observed for weed density and *H*', the densities of the dominant weed species increased with precipitation, showing an increase from season 2020 (low precipitation) to 2019 and 2021 (medium and high precipitation) (Fig. S4). The density of BIDPI was the highest in the NT+M system and the lowest in the NT+R system (*i.e.*, approximately 42 times higher in NT+M than NT+R) (Table S3). Application of mulching either to CT or NT (CT+M or NT+M) promoted GASPA, whereas CT promoted RCHSC as compared to CT+R and CT+M+R. At the clay location (UZ), the application of all three CA components resulted in highest densities of BIDPI (Table S3) (NT+M+R ≠ CT). As also observed for the sandy location, GASPA was promoted by the application of mulching irrespective of the tillage type (CT+M and NT+M), also along with rotation (CT+M+R and NT+M+R). Accordingly, LEUMAR and RCHSC were promoted by the application of mulching irrespective of the tillage type.

3.3. *Effect of season and cropping system on weed community structure*

Both season and cropping system significantly modified weed community structure at both locations (Table 2; Fig. 2).

Season acted as stronger driver than cropping system based on the percentage of total explained variance (Table 2). Pairwise comparisons indicated distinct weed community structures for each season (Table 3), and this was confirmed by the PCoA plots at both locations (Fig. 2a,c,e, g). Moreover, the dispersion of the field replicates from group centroid,

Table 2

Permutational multivariate analysis of variance (PERMANOVA) results for the effect of season, cropping system and their interaction on weed community structure at Domboshawa Training Centre (DTC; sandy location) and at University of Zimbabwe (UZ; clay location).

Location	Source	DF	Pseudo-*F*	*P* (MC)[†]	Explained variation (%)
DTC	Season[‡]	2	45.949	**0.001**	55.90
	System[‡]	7	2.047	**0.003**	3.47
	Season × System	14	1.083	0.321	0.83
UZ	Season	2	10.595	**0.001**	21.27
	System	7	2.528	**0.001**	9.03
	Season × System	14	0.930	0.670	-1.25

[†] *P* values based on Monte-Carlo permutational test, *P*(MC); [‡] Three seasons and eight cropping systems (see Table S1).

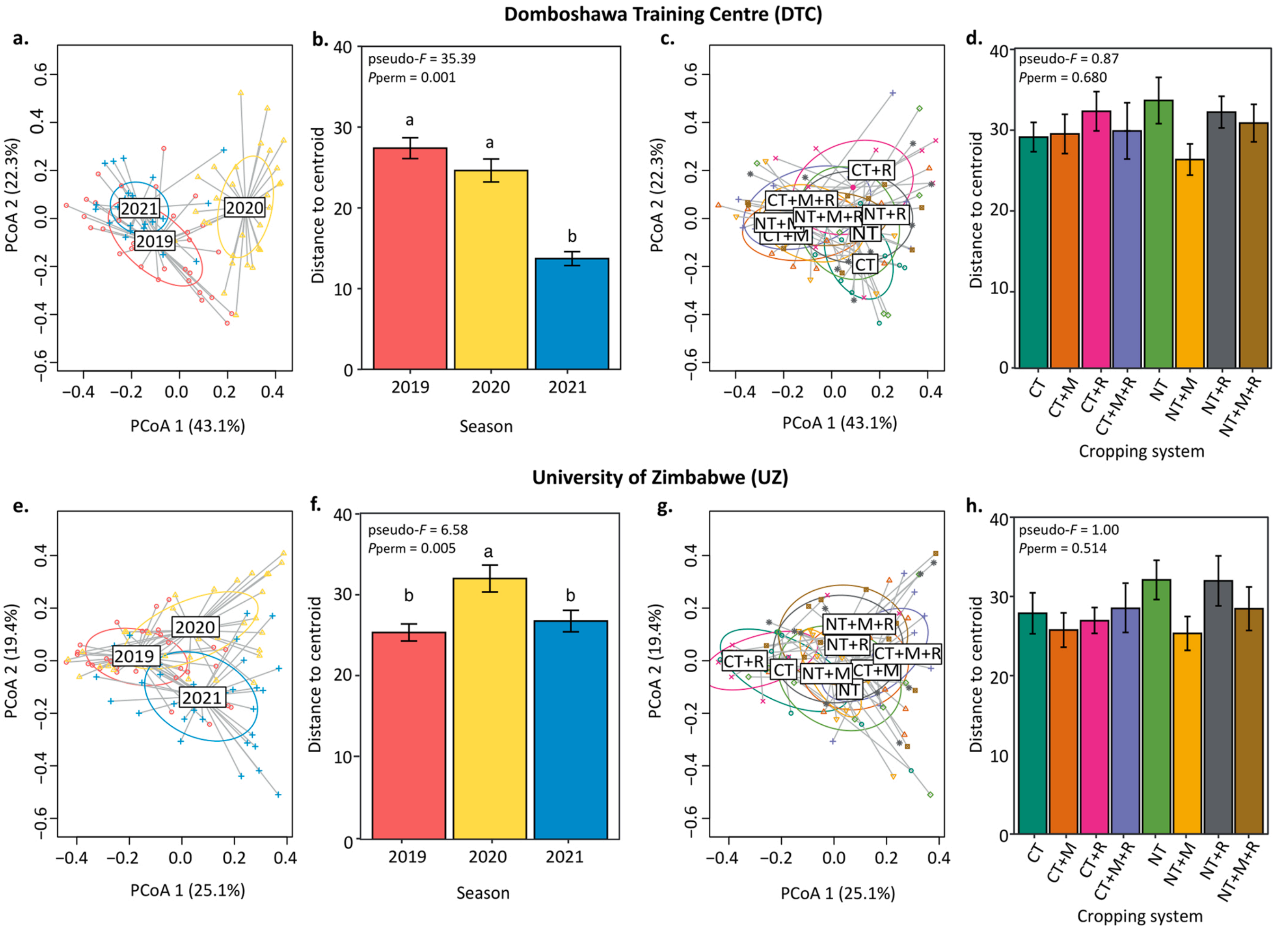

Fig. 2. Principle coordinates analysis (PCoA) based on Bray-Curtis distance dissimilarity of fourth-root transformed weed community relative abundances. Plots show differences among seasons and cropping systems at Domboshawa Training Centre (DTC; sandy location) (a and c), and at University of Zimbabwe (UZ; clay location) (e and g) (see Table 2). Permutational dispersion (PERMDISP) tests on the same data matrices at DTC and UZ (season: b and f; cropping system: d and h) are represented by distances of objects from the centroid and standard error (SE). Values correspond to the mean distance of the group samples to the group centroids for seasons and cropping systems at DTC (b and d), and at UZ (f and h). Abbreviations of the cropping systems are: CT, conventional tillage; CT+M, CT plus mulching; CT+R, CT plus crop rotation; CT+M+R, CT plus mulching and rotation; NT, no-tillage; NT+M, NT plus mulchng; NT+R, NT plus rotation; NT+M+R, NT plus mulching and rotation. Columns with different letters are significantly different based on the reported P-permutational values (*P*perm).

measured as mean distance, highlighted significant differences only among seasons (Fig. 2b,d,f,h). At DTC, the weed community structure in the seasons 2019 and 2020 (low and medium precipitation) had higher dispersion than in 2021 (high precipitation), while at UZ it had higher dispersion in 2020 (medium precipitation) than in 2019 and 2021 (low and high precipitation) (Fig. 2b,f). At both locations, the pairwise comparisons of the weed community structure revealed significant differences among various pairs of cropping systems (Table 3). At both locations, the implementation of crop rotation and mulching either in NT or CT systems resulted in the modification of the structure of weed community respect to CT and NT alone. In the PCoA plots of both locations, the centroids of the CT and CT+R systems showed a clear separation from the rest of the cropping systems on the ordination space (Fig. 2c, g).

The similarity analysis (SIMPER) revealed that on average 12 species contributed to the observed differences in the weed community structures for cropping system and season at both locations, but species identity varied among treatments (Fig. 3). Overall, eight weed species common for both locations [BIDPI; COMBE; *Cyperus esculentus* L. (CYPES), *Eleusine indica* (L.) Gaertn. (ELEIN); *Erigeron sumatrensis* Retz. (ERISU), GASPA; LEUMAR; RCHSC] were responsible for most of community structure differences among cropping systems. The relative abundances of these weed species accounted for approximately 69 % and 86 % of the observed differences in DTC and UZ, respectively. Moreover, four weed species common for both locations (BIDPI; COMBE; GASPA; RCHSC) were responsible for the community structure differences among seasons. Indeed, the relative abundances of these weed species accounted for *ca.* 56 % and 59 % of the observed differences in DTC and UZ, respectively.

3.4. Effect of cropping system on maize productivity and relationship with precipitation and weed parameters

Maize grain yield and stover differed among seasons and cropping systems at both locations (Table 1). At DTC (sandy location), there was a decrease in grain yield with 2021 (having the highest precipitation) showing the lowest grain yield and biomass (Fig. 4a). Averaged across seasons, the CT+M+R system resulted in the highest grain yield and stover, whereas the NT system resulted in the lowest values (Fig. 4b). At UZ (clay location), there was an increase of grain yield with 2021 (having the highest precipitation) showing the highest grain yield and stover (Fig. 4c). Moreover, the C+M+R and NT+M+R systems had the highest grain yield and stover, whereas the CT and NT systems showed the lowest yield (Fig. 4d).

Table 3

Permutational multivariate analysis of variance (PERMANOVA) pairwise comparisons on weed community structures under different cropping systems (systems) and seasons at the Domboshawa Training Centre (DTC; sandy location) and University of Zimbabwe (UZ; clay location).

	DTC		UZ	
Pairs (Systems & seasons)[†]	Pseudo-*F*	*P* (MC)[‡]	Pseudo-*F*	*P* (MC)[‡]
CT *vs* CT+M	1.070	**0.015**	1.975	**0.048**
CT *vs* CT+M+R	0.927	**0.020**	2.391	**0.014**
CT *vs* CT+R	0.884	0.150	1.705	**0.042**
CT *vs* NT	0.512	0.675	1.19	0.205
CT *vs* NT+M	1.405	**0.007**	2.293	**0.019**
CT *vs* NT+M+R	0.734	0.116	2.422	**0.018**
CT *vs* NT+R	0.745	0.196	1.154	0.082
CT+M *vs* CT+M+R	0.694	0.183	0.230	0.933
CT+M *vs* CT+R	1.524	**0.019**	3.933	**0.003**
CT+M *vs* NT	1.198	**0.027**	2.122	**0.045**
CT+M *vs* NT+M	0.246	0.288	1.786	0.088
CT+M *vs* NT+M+R	0.504	0.279	1.505	0.167
CT+M *vs* NT+R	1.028	**0.045**	2.112	**0.028**
CT+M+R *vs* CT+R	0.535	0.360	4.238	**0.003**
CT+M+R *vs* NT	0.523	0.151	1.708	0.098
CT+M+R *vs* NT+M	0.634	0.129	1.84	0.093
CT+M+R *vs* NT+M+R	0.327	0.461	0.985	0.653
CT+M+R *vs* NT+R	0.816	0.067	1.594	0.091
CT+R *vs* NT	0.338	0.605	2.568	**0.004**
CT+R *vs* NT+M	1.656	**0.011**	2.842	**0.007**
CT+R *vs* NT+M+R	0.609	0.302	2.280	**0.027**
CT+R *vs* NT+R	0.516	0.363	2.765	**0.002**
NT *vs* NT+M	1.092	0.067	2.214	0.154
NT *vs* NT+M+R	0.439	0.356	2.575	0.067
NT *vs* NT+R	0.825	0.146	1.394	0.078
NT+M *vs* NT+M+R	0.478	0.145	1.231	0.097
NT+M *vs* NT+R	1.594	**0.003**	2.034	**0.026**
NT+M+R *vs* NT+R	0.432	0.317	1.729	0.154
2019 *vs* 2020	44.151	**0.001**	6.092	**0.001**
2019 *vs* 2021	45.294	**0.001**	12.09	**0.001**
2020 *vs* 2021	106.599	**0.001**	9.293	**0.001**

[†] Abbreviations of the cropping systems are: CT, conventional tillage; CT+M, CT plus mulching; CT+R, CT plus crop rotation; CT+M+R, CT plus mulching and rotation; NT, no-tillage; NT+M, NT plus mulching; NT+R, NT plus rotation; NT+M+R, NT plus mulching and rotation.[‡] *P* values based on Monte-Carlo permutational test. Pairs with significant differences are written in bold.

Structural equation modelling resulted in significant fit at both locations (Fig. 5). At the DTC (sandy location), precipitation did not affect grain yield, whereas a significant and positive relationships was observed with weed density ($\lambda = 0.86$), diversity (H') ($\lambda = 1.09$), evenness (J') ($\lambda = 0.41$), and richness (D_{mg}) ($\lambda = 0.69$) (Fig. 5a). Weed density negatively affected H' and J' ($\lambda = -0.64$ and -0.56, respectively). Positive covariations were observed between H' with J' ($\lambda = 0.57$), and D_{mg} ($\lambda = 0.53$), while a negative covariance was observed between J', and D_{mg} ($\lambda = -0.29$). Of all the measured parameters, only H' showed a significant and positive effect on maize grain yield ($\lambda = 0.65$). At UZ (clay location), precipitation showed.

a significant and positive effect on grain yield ($\lambda = 0.65$), whereas no direct effects were observed on weed density and J' (Fig. 5b). Moreover, differently from DTC, at UZ a significant and negative relationship was observed between precipitation and H' ($\lambda = -0.25$) and D_{mg} ($\lambda = -0.64$). Similarly, to DTC weed density at UZ negatively affected H' and J' ($\lambda = -0.23$ and -0.39, respectively), and positive covariations were observed between H' with J' ($\lambda = 0.90$), and D_{mg} ($\lambda = 0.58$). However, a positive covariance was observed between J' and D_{mg} ($\lambda = 0.21$). As expected, an increase in weed density resulted in a decrease in maize grain yield ($\lambda = -0.23$). Contrary to what was observed at the DTC, precipitation had a negative impact on D_{mg} ($\lambda = -0.64$).

4. Discussion

4.1. Season and cropping system explain weed density and community diversity

The occurrence and proliferation of weeds at a particular location is determined by different abiotic and biotic factors, and these include soil type, cropping system, and climate (Pyšek et al., 2002, 2005). However, these factors do not affect weed occurrence independently, but interact, and thus the role played by each one of them is difficult to be assessed (Pyšek et al., 2002). We encountered weeds which are referred to as "indicator plants" or "bioindicator plants" whose occurrence is shaped by edaphic and climatic factors. For example, *A. hybridus* (MACH) is a species that prefers well drained soils, and this may explain its prevalence at the sandy location (DTC). Species, such as the *I. purpurea* (PHBPU)*,* prefer soils that are high in organic matter and hence it was observed at the clay location (UZ) having high organic matter. Thus, in our study, there was a notable difference in the weed species that appeared at the sandy and clay locations, as well as in different seasons.

Precipitation influenced weed density and community diversity at the sandy location (DTC). The effect was higher on weed density than on community diversity. Both parameters increased with increasing precipitation and this is because weeds, like other plants, depend on water availability for their emergence and growth (Robinson and Gross, 2010). The increase in weed community diversity with precipitation can be explained by the emergence of new weed species, increase in number of rarer species, or decrease in abundance of the dominant species (Shannon and Weaver, 1949). In our study, this relationship can be explained by a small but significant increase in weed numbers as shown by the trends of individual species abundance as well as by the increase in weed species richness. A focus on the weed species richness showed that medium-high precipitation increased the richness irrespective of cropping systems, and that the application of mulching to NT in seasons with low precipitation resulted in the richest communities. High rainfall and the preservation of moisture due to mulching reduced the competition for essential resources between the weed species (Ulber et al., 2009) Furthermore, NT and light hoe weeding ensured that weed seeds were buried in the shallow soil profile which was more conducive for germination as opposed to deep burying in tillage-based systems (Santín-Montanyá et al., 2020).

In the less drained and more fertile clay soils (UZ) where rainfall was generally lower, NT coupled with mulching promoted weed density in the season with the lowest rainfall. Across the seasons, the same system resulted in the highest community diversity. These responses can be attributed to the increase in abundance of weed species (*e.g.*, *G. parviflora,* GASPA) and to the emergence of new species in this system because of moisture conservation and absence of tillage. Moreover, these responses can be linked to the increase of soil organic matter found in the same site under NT+M (Mhlanga et al., 2022). Contrary to our findings, in other studies, mulching was shown to provide a physical barrier that impeded weed germination and hence reduced weed densities (Mhlanga et al., 2015; Zhang et al., 2021). Thus, mulching can lead to shifts in weed communities over time. Due to the rate of maize mulch that was applied in our study and its coarseness, we presume that shifts in weed communities were as an effect of moisture conservation rather than as a physical barrier. However, the high community diversity we observed in mulch system points to a less competitive community as there is no dominance of certain species. This means that weed control in such systems is more flexible rather than rigid and not skewed towards the control of dominant weeds (Storkey and Neve, 2018). The decrease in weed richness with increasing precipitation at the clay location may be attributed to the fact that the clay soil is poorly drained and hence prone to waterlogging, creating anaerobic soil conditions and poor weed seed germination (Robinson and Gross, 2010).

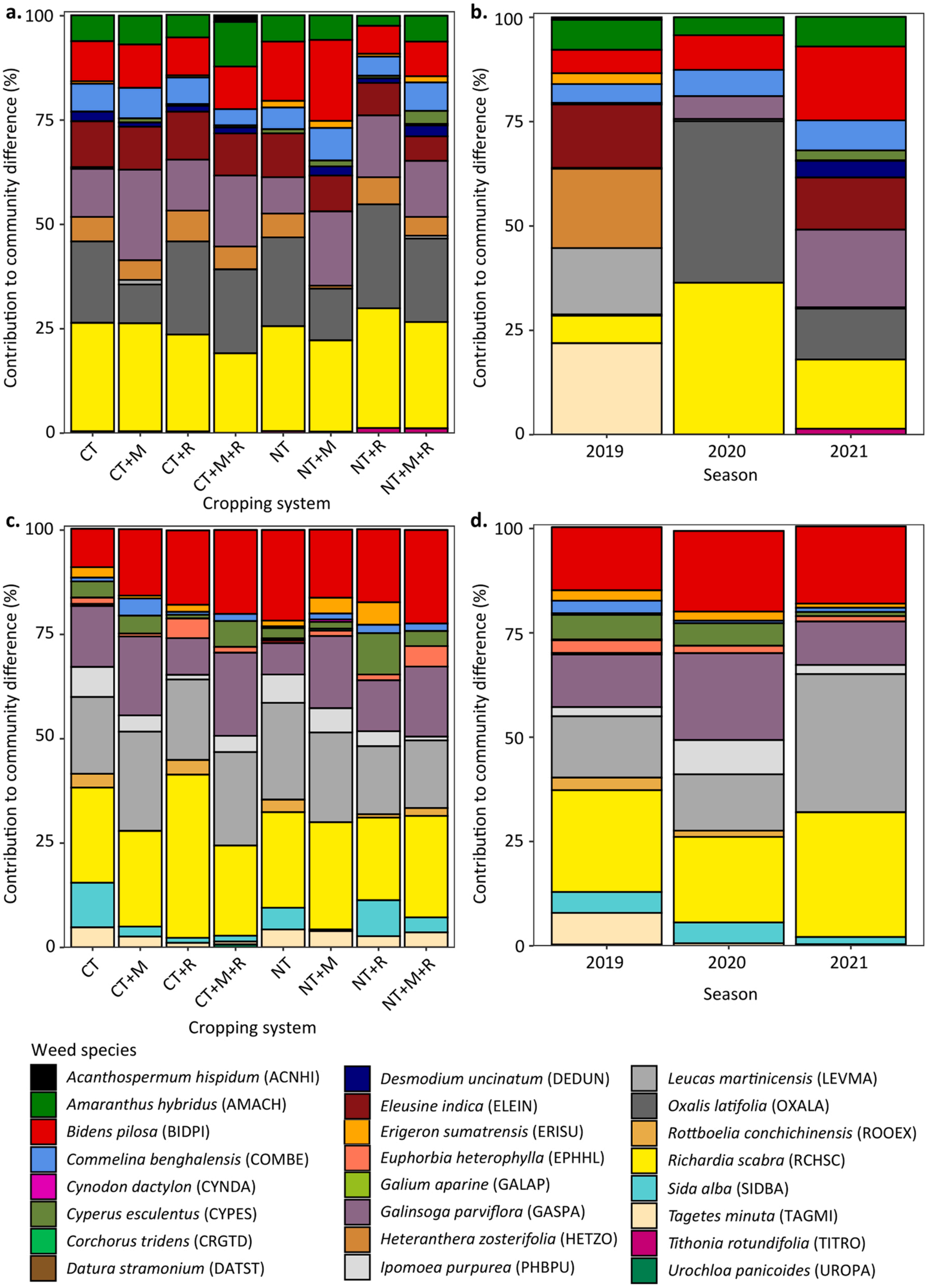

Fig. 3. Similarity percentages analysis (SIMPER) identifying the weed species that were responsible for community structure differences among the cropping systems and the seasons at Domboshawa Training Centre (DTC; sandy location) (a and b), and at University of Zimbabwe (UZ; clay location) (c and d). The listed species explain 100 % of the contribution. Abbreviations of the cropping systems are: CT, conventional tillage; CT+M, CT plus mulching; CT+R, CT plus crop rotation; CT+M+R, CT plus mulching and rotation; NT, no-tillage; NT+M, NT plus mulching; NT+R, NT plus rotation; NT+M+R, NT plus mulching and rotation. The abbreviations in parenthesis in front of each weed species name are based on the European and Mediterranean Plant Protection Organization (EPPO) coding.

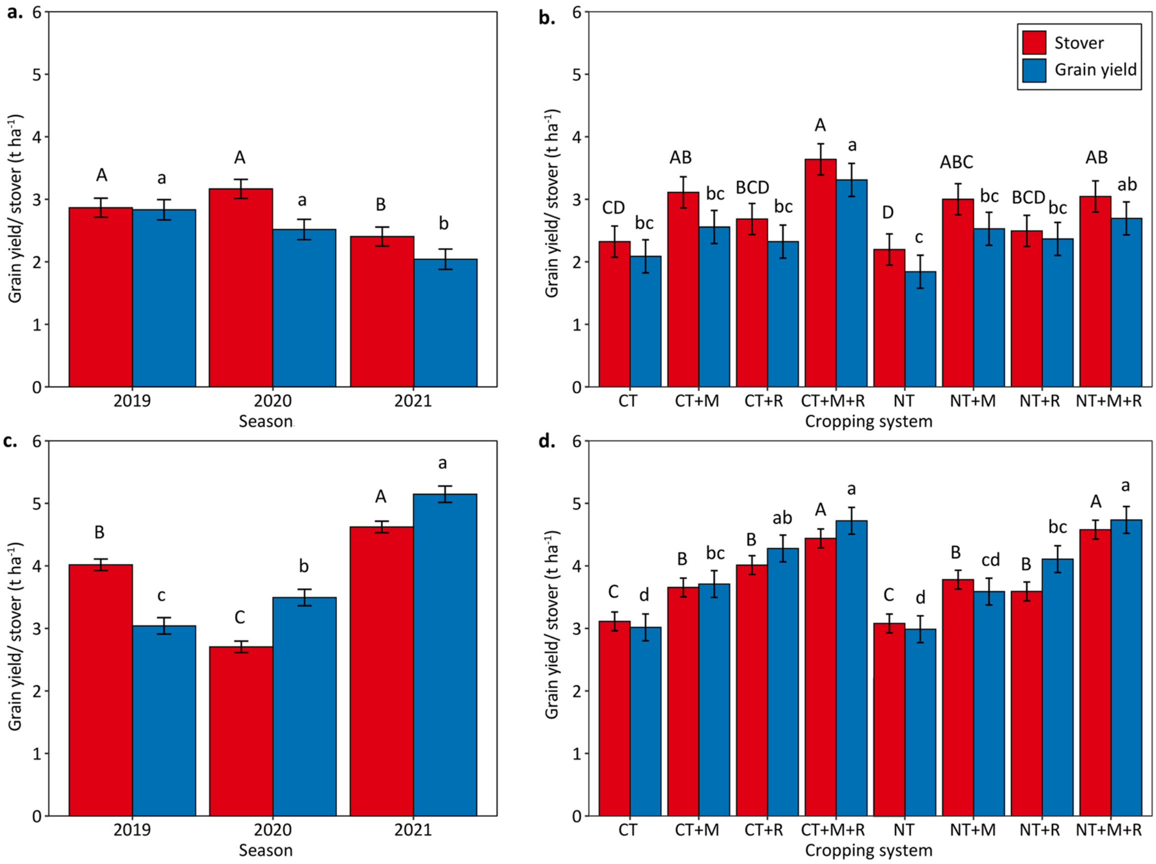

Fig. 4. Effect of season and cropping system on maize grain yield and stover at Domboshawa Training Centre (DTC; sandy location) (a and b), and at University of Zimbabwe (UZ; clay location) (c and d). Columns with different letters are significantly different from each other based on the *P*-values reported in Table 1. The uppercase letters are for mean comparison for stover (biomass), and the lowercase letters are for mean comparison for grain yield. Abbreviations of cropping systems: CT, conventional tillage; CT+M, CT plus mulching; CT+R, CT plus crop rotation; CT+M+R, CT plus mulching and rotation; NT, no-tillage; NT+M, NT plus mulching; NT+R, NT plus rotation; NT+M+R, NT plus mulching and rotation.

4.2. Season and cropping system shape weed community structures

Season and cropping system shaped weed community structure at both locations. Inter-seasonal differences however were more influential than the cropping system. These results are in line with the findings of Derksen et al. (1993) in which weed community response was more influenced by seasonal variations than by tillage system. The amount of precipitation and its seasonal distribution were variable and this affected weed seed germination and development, and may explain the stronger differences in the resulting weed communities across the seasons compared to cropping system (Sánchez et al., 2014). Water availability has been shown to have high effects on plant community productivity and species composition due to specific germination requirements (Suttle et al., 2007). These variable germination requirements account for the variability in the species that contributed to the community differences, as shown by the similarity percentage analysis. Weeds that can thrive under different conditions, such as *R. scabra* (RCHSC)and *G. parviflora* (GASPA), were more responsible for the community structure differences since they appeared in all seasons. Such weeds are considered as “core” species in our study owing to their high colonization ability, copious seed production, and ability to grow alongside crops (Mohler, 2001; Magurran and Henderson, 2003). However, there were also weeds that require specific germination conditions, such as *A. hispidum* (CNHI)*,* and these appeared in certain seasons. As an example, in our study, the season 2020 which had low to medium rainfall resulted in unique weed community structures at both locations, with fewer species contributing to majority of community differences.

Furthermore, cropping system resulted in different weed community structures. At both locations, the implementation of rotation and mulching either in NT or CT systems resulted in the modification of the structure of weed community with respect to CT and NT alone. Modification of cropping systems, especially through changing cropping sequences and including mulching, alters weed species composition (Koocheki et al., 2009; Zhang et al., 2021). The integration of vigorously growing crops, such as cowpea, in crop rotations exerts more competition for water and nutrients on weeds as compared to cereals, such as maize. This competition leads to a shift in the weed communities that emerge, favouring those species (*e.g.*, *B. pilosa,* IDPI) that are adapted to growing alongside other competitive crops (Mhlanga et al., 2016). A study by Cardina et al. (2002) showed that crop rotation was a more important determinant of weed seed density than tillage. Due to the variability in type of crops, life cycles, and weed management in rotations, there are more opportunities for weed mortality as compared to monocultures (Martin and Felton, 1993). These variabilities may also provide more chances for emergence and establishment of weeds in rotations than in monocultures and hence the balance is reflected in the resulting weed communities (Dorado et al., 1999).

Besides the effect of cropping systems and seasons on weed communities, the application of glyphosate at the beginning of each season throughout the experimental period may have also shaped weed communities with possible selection for glyphosate-resistant species (Heap and Duke, 2018). These species included the *B. pilosa* (IDPI), *A. hybridus* (MACH), and *E. indica* (LEIN) which were prevalent at the study sites. However, this herbicidal effect was not elucidated in our study.

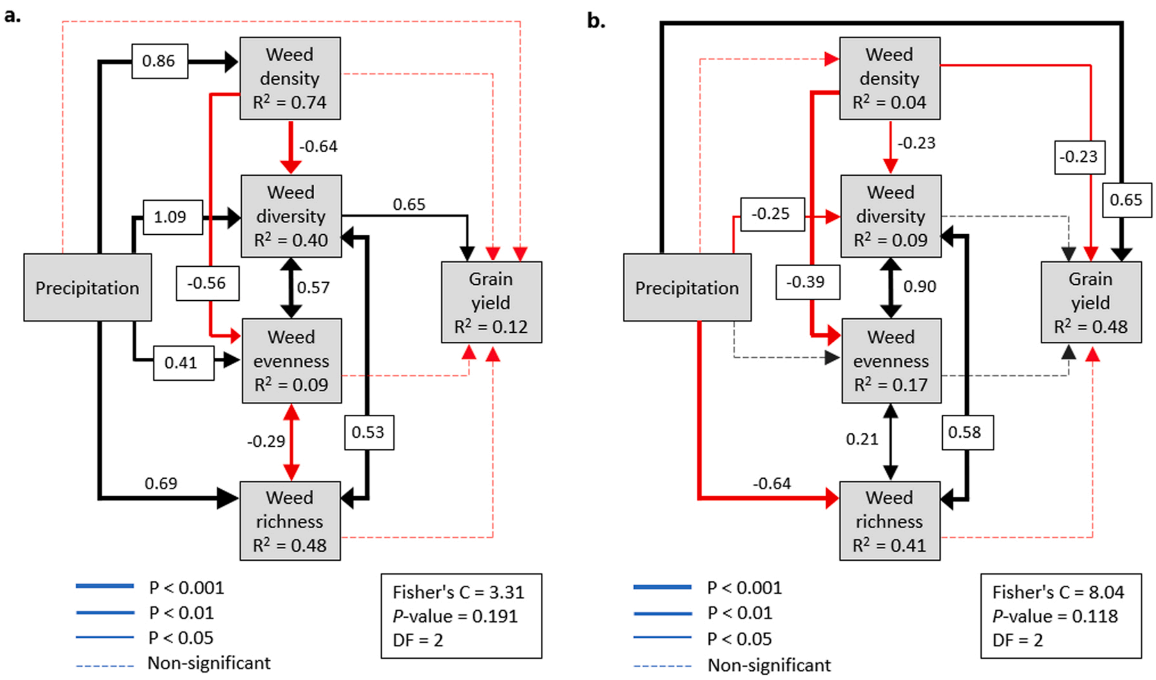

Fig. 5. Structural equation model (SEM) (path analysis) of the precipitation effect on weed parameters [weed density, weed community diversity (Shannon diversity, *H'*), weed evenness Pielou evenness, *J'*), weed richness (Margalef richness, *Dmg*)] and maize grain yield at Domboshawa Training Centre (DTC; sandy location) (a), and University of Zimbabwe (UZ; clay location) (b), across 2019, 2020, and 2021. The black lines represent positive influence, while the red lines represent negative influence. Solid lines and dashed lines represent significant ($P < 0.05$) and non-significant ($P > 0.05$) influences, respectively. Standardized path coefficients are reported for each effect pathway.

4.3. Maize yield response and its relationship with cropping system, precipitation and weed traits

The use of mulching and rotation either under NT or tillage resulted in similar yield responses. These responses are in line with the findings of Mhlanga et al. (2021) in a multilocational study across SAA in previous seasons in which our experiments were included. In the previous study, mulching was identified as crucial in yield improvement, and this could be due to its ability to conserve moisture since water availability is one of the major limitations to production. In addition, crop rotation with legumes can also be seen as a crucial practice in yield improvement, as the inclusion of legume crops, such as cowpea that biologically fix N and produce large quantities of biomass (Haynes et al., 1993; Mariotti et al., 2015), add N-rich labile organic matter to soil which is easily decomposed by specific N-cycling microbial community (Ciccolini et al., 2016a; b). Both mulching and crop rotation may have a suppressive effect on weeds with a positive reduction of their competition (Nichols et al., 2015). Thus, combining mulching and rotation will reduce the competitive effects of the weeds while aiding in organic matter build-up in the soil and thus, increasing the yield of maize.

Precipitation positively increased weed density and weed community diversity parameters only at the sandy soil location (DTC), while at the clay soil location (UZ) it had negative impacts. These differences in weed parameter responses may be attributed to the differences in weed (floral) communities at these locations which respond differently to water availability (Robinson and Gross, 2010). This can also explain the differences in the influence of weed parameters on maize grain yield at the two locations. Weed community diversity exerted a positive influence on grain yield at the sandy location. Indeed, more diverse weed communities are less prone to the dominance of certain weed species which are usually more adapted and competitive to crops (Storkey and Neve, 2018). Less diverse cropping systems, such as monocultures, are usually dominated by highly adapted and widely distributed weed species, and such species present huge niche competition resulting in lower crop yields. Conversely, weed density showed a negative influence on maize grain yield due to the increased competitive ability for water, light, and mineral resources, as well as allelopathy and parasitism (De Bertoldi et al., 2009; Korres, 2018). However, these findings should be confirmed through specific experimental designs imposing a wider interval of weed diversity.

5. Conclusion

Understanding how weed communities respond to CA practices is important in agroecosystem management. Here, for the first time, we assessed how weed communities responded to different combinations of CA components (*i.e.*, no-tillage, crop rotation, and mulching) in Southern Africa. Weed community structure was influenced by both seasonal variations and cropping systems, but precipitation was the principal driver differentially acting in the two locations. Overall, at the sandy location, precipitation significantly and positively affected weed density and community diversity, whereas cropping system did not affect these traits. Weed richness was highest with the implementation of mulching to no-tillage at medium-high precipitation. At the clay location, an opposite pattern was observed. Weed density was lower in seasons with medium-high precipitations than under low precipitation, when NT+M showed the highest weed density in response to increased moisture retention. Weed community diversity was highest under NT+M, whereas weed species richness decreased with high precipitation. At both locations, the implementation of mulching and rotation either in NT or CT systems resulted in the modification of the structure of weed community with respect to CT and NT alone, and these CA combinations were associated with highest maize grain yield. Finally, the structure of the models describing the response of maize yield to precipitation and weed community diversity differed between locations. The novel finding is that at the sandy location weed community diversity was positively associated to maize grain yield, whereas at the clay location this relationship was not demonstrated. However, we must acknowledge that some confounding effects, such as rainfall and cropping system, affecting maize yield, might weaken the causal effect between weed diversity and maize yield, turning it to coexistence. These new insights support the need in Southern Africa to implement rotation and mulching either in no-tillage or conventional tillage allowing the promotion of diverse weed communities in order to support crop yield.

Ethics approval

All ethics committees of the organizations with which the authors are affiliated have no objections to the publication of this work.

Consent for publication

Not applicable.

Author contribution

Author contributions: Experiment idea and set-up of trials, C.T.; coordination of data collection, C.T., B.M., L.E., E.P.; formal data analysis, B.M., E.P; writing original manuscript draft, B.M., EP; writing, review, and editing, E.P., L.E., C.T. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

The PhD fellowship for BM was funded by the Scuola Superiore Sant'Anna. All the authors are grateful to the International Maize and Wheat Improvement Centre for funding the setup and running of the experimental trials and to donors of the MAIZE CGIAR Research Program (www.maize.org) who supported the trials until 2018. The authors are thankful of the DSCATT Project for co-funding the CIMMYT step-trials since 2018. The DSCATT project (N° AF 1802-001, N° FT C002181) is funded by the Agropolis Foundation (through the "Programme Investissement d'Avenir" Labex Agro, funding ANR-10-LABX-0001-01) and by the TOTAL Foundation, as part of a sponsorship agreement. The authors would like to thank also the project Africa Research in Sustainable Intensification for the Next Generation (Africa RISING, AID-BFS-G-11-00002) for co-funding the CIMMYT step-trials. The financial support of the Project PSR 2014- 2020 - Misura 16.2 PS-GO 2017 - Progetto AGROCIRCOLIVE – CUP ARTEA 831728 is gratefully acknowledged. Special thanks go to the technical teams at the two experimental locations, led by Sign Phiri and Herbert Chipara that assisted in data collection.

Availability of data and R code

Data used in this study are stored in a public data repository and can be made available upon reasonable request following data-sharing regulations. The R scripts used in data analyses are available from the corresponding author upon request. Sequences generated in this study were uploaded in the NCBI database (submission number SUB10794739) and accession numbers OM049043-OM049185.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2022.108724.

References

Adeux, G., Vieren, E., Carlesi, S., Bàrberi, P., Munier-Jolain, N., Cordeau, S., 2019. Mitigating crop yield losses through weed diversity. Nat. Sustain 2, 1018–1026. https://doi.org/10.1038/s41893-019-0415-y.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/10.1046/j.1442-9993.2001.01070.x.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-e, Auckland, New Zealand.

Baker, C., Madakadze, I.C., Swanepoel, C.M., Mavunganidze, Z., 2018. Weed species composition and density under conservation agriculture with varying fertiliser rate. S. Afr. J. Plant Soil 35, 329–336. https://doi.org/10.1080/02571862.2018.1431814.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Botha, A., 2010. Common Weeds of Crops and Gardens in Southern Africa, 2nd ed. Agricultural Research Council,, South Africa.

Bray, J.R., Curtis, J.R.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.

Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. Agron. Sustain. Dev. 35, 891–909. https://doi.org/10.1007/s13593-015-0302-5.

Cardina, J., Herms, C.P., Doohan, D.J., 2002. Crop rotation and tillage system effects on weed seedbanks. Weed Sci. 50, 448–460.

Ciccolini, V., Bonari, E., Ercoli, L., Pellegrino, E., 2016a. Phylogenetic and multivariate analyses to determine the effect of agricultural land-use intensification and soil physico-chemical properties on N-cycling microbial communities in drained Mediterranean peaty soils. Biol. Fert. Soils 52, 811–824. https://doi.org/10.1007/s00374-016-1121-9.

Ciccolini, V., Ercoli, L., Davison, J., Vasar, M., Öpik, M., Pellegrino, E., 2016b. Land-use intensity and host plant simultaneously shape the composition of arbuscular mycorrhizal fungal communities in a Mediterranean drained peatland. FEMS Microbiol. Ecol. 92, fiw186. https://doi.org/10.1093/femsec/fiw186.

Clarke, K.R., Gorley, R.N., Somerfield, P.J., Warwick, R.M., 2014a. Change in marine communities: an approach to statistical analysis and interpretation, 3rd ed. PRIMER-E Ltd, Plymouth, UK: Plymouth Marine Lab.

Clarke, K.R., Tweedley, J.R., Valesini, F.J., 2014b. Simple shade plots aid better long-term choices of data pre-treatment in multivariate assemblage studies. J. Mar. Biol. Assoc. UK 94, 1–16.

Dahlin, A.S., Rusinamhodzi, L., 2019. Yield and labor relations of sustainable intensification options for smallholder farmers in sub-Saharan Africa. A meta-analysis. Agron. Sustain. Dev. 39, 32. https://doi.org/10.1007/s13593-019-0575-1.

De Bertoldi, C., De Leo, M., Braca, A., Ercoli, L., 2009. Bioassay-guided isolation of allelochemicals from *Avena sativa* L.: allelopathic potential of flavone C-glycosides. Chemoecology 19, 169–176. https://doi.org/10.1007/s00049-009-0019-5.

Derksen, D.A., Lafond, G.P., Thomas, A.G., Loeppky, H.A., Swanton, C.J., 1993. Impact of agronomic practices on weed communities: tillage systems. Weed Sci. 41, 409–417.

Dorado, J., Monte, J.P.D., López-Fando, C., 1999. Weed seedbank response to crop rotation and tillage in semiarid agroecosystems. Weed Sci. 47, 67–73. https://doi.org/10.1017/S0043174500090676.

Ekeleme, F., Jibrin, J.M., Kamara, A.Y., Oluoch, M., Samndi, A.M., Fagge, A.A., 2014. Assessment of the relationship between soil properties, Striga hermonthica infestation and the on-farm yields of maize in the dry Savannas of Nigeria. Crop Prot. 66, 90–97. https://doi.org/10.1016/j.cropro.2014.09.001.

El Omari, B., El Ghachtouli, N., 2021. Arbuscular mycorrhizal fungi-weeds interaction in cropping and unmanaged ecosystems: a review. Symbiosis 83, 279–292. https://doi.org/10.1007/s13199-021-00753-9.

Ercoli, L., Masoni, A., Mariotti, M., Pampana, S., Pellegrino, E., Arduini, I., 2017. Effect of preceding crop on the agronomic and economic performance of durum wheat in the transition from conventional to reduced tillage. Eur. J. Agron. 82, 125–133. https://doi.org/10.1016/j.eja.2016.10.010.

FAO, 2019. Conservation Agriculture. Available online at: 〈http://www.fao.org/conservation-agriculture/overview/what-is-conservation-agriculture/en/〉 (Accessed August 2019).

Ferrero, R., Lima, M., Davis, A.S., Gonzalez-Andujar, J.L., 2017. Weed diver- sity affects soybean and maize yield in a long term experiment in Michigan, USA. Front. Plant Sci. 8, 236 2017, 00236. https://doi.org/10.3389/fpls.

Fonteyne, S., Singh, R.G., Govaerts, B., Verhulst, N., 2020. Rotation, Mulch and Zero tillage reduce weeds in a long-term conservation agriculture trial. Agronomy 10. https://doi.org/10.3390/agronomy10070962.

Franke, A.C., van den Brand, G.J., Vanlauwe, B., Giller, K.E., 2018. Sustainable intensification through rotations with grain legumes in Sub-Saharan Africa: a review. Agric. Ecosyst. Environ. 261, 172–185. https://doi.org/10.1016/j.agee.2017.09.029.

Haynes, R.J., Martin, R.J., Goh, K.M., 1993. Nitrogen fixation, accumulation of soil nitrogen and nitrogen balance for some field-grown legume crops. Field Crop. Res. 35, 85–92. https://doi.org/10.1016/0378-4290(93)90141-9.

Heap, I., Duke, S.O., 2018. Overview of glyphosate-resistant weeds worldwide. Pest Manag. Sci. 74, 1040–1049. https://doi.org/10.1002/ps.4760.

IUSS Working Group WRB, 2015. World Reference Base on Soils (World Soil Resources Reports No. 106), International soil classification system for naming soils and creating legends for soil maps. FAO-ISRIC, Rome, Italy.

Kodzwa, J.J., Gotosa, J., Nyamangara, J., 2020. Mulching is the most important of the three conservation agriculture principles in increasing crop yield in the short term, under sub humid tropical conditions in Zimbabwe. Soil Till. Res. 197, 104515 https://doi.org/10.1016/j.still.2019.104515.

Koocheki, A., Nassiri, M., Alimoradi, L., Ghorbani, R., 2009. Effect of cropping systems and crop rotations on weeds. Agron. Sustain. Dev. 29, 401–408. https://doi.org/10.1051/agro/2008061.

Korres, N.E., 2018. Chapter 6 - Agronomic weed control: a trustworthy approach for sustainable weed management. In: Jabran, K., Chauhan, B.S. (Eds.), Non-Chemical Weed Control. Academic Press, pp. 97–114. https://doi.org/10.1016/B978-0-12-809881-3.00006-1.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. Meteorol. Z. 15, 259–263. 〈https://10.1127/0941-2948/2006/0130〉.

Lee, N., Thierfelder, C., 2017. Weed control under conservation agriculture in dryland smallholder farming systems of southern Africa. A review. Agron. Sustain. Dev. 37, 48. https://doi.org/10.1007/s13593-017-0453-7.

Lefcheck, J., 2016. piecewiseSEM: piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579. https://doi.org/10.1111/2041-210X.12512.

Lenth, R., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.4. 〈https://CRAN.R-project.org/package=emmeans〉.

MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., Dehnen-Schmutz, K., 2020. An ecological future for weed science to sustain crop production and the environment. A review. Agron. Sustain. Dev. 40, 1–29. https://doi.org/10.1007/s13593-020-00631-6.

Magurran, A.E., 2004. Measuring Biological Diversity. John Wiley & Sons, New Jersey, USA.

Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422, 714–716. https://doi.org/10.1038/nature01547.

Mahgoub, A.M.M.A., 2019. The impact of five environmental factors on species distribution and weed community structure in the coastal farmland and adjacent territories in the northwest delta region, Egypt. Heliyon 5, e01441.

Makanganise, A., Mabasa, S., 1999. Field Guide to the Identification of Important Weeds of Arable Lands in Zimbabwe. Department of Research and Specialist Services, Harare, Zimbabwe.

Margalef, R., 1972. Homage to Evelyn Hutchinson, or why there is an upper limit to diversity. Connecticut Academy of Arts and Sciences.

Mariotti, M., Masoni, A., Ercoli, L., Arduini, I., 2015. Nitrogen leaching and residual effect of barley/field bean intercropping. Plant Soil Environ. 61, 60–65. https://doi.org/10.17221/832/2014-PSE.

Martin, R., Felton, W., 1993. Effect of crop rotation, tillage practice, and herbicides on the population dynamics of wild oats in wheat. Aust. J. Exp. Agric. 33, 159–165.

Mhlanga, B., Cheesman, S., Maasdorp, B., Muoni, T., Mabasa, S., Mangosho, E., Thierfelder, C., 2015. Weed community responses to rotations with cover crops in maize-based conservation agriculture systems of Zimbabwe. Crop Prot. 69, 1–8. https://doi.org/10.1016/j.cropro.2014.11.010.

Mhlanga, B., Cheesman, S., Chauhan, B.S., Thierfelder, C., 2016. Weed emergence as affected by maize-cover crop rotations in contrasting arable soils of Zimbabwe under conservation agriculture. Crop Prot. 81, 47–56. https://doi.org/10.1016/j.cropro.2015.12.007.

Mhlanga, B., Ercoli, L., Pellegrino, E., Onofri, A., Thierfelder, C., 2021. The crucial role of mulch to enhance the stability and resilience of cropping systems in southern Africa. Agron. Sustain. Dev. 41, 29. https://doi.org/10.1007/s13593-021-00687-y.

Mhlanga, B., Pellegrino, E., Thierfelder, C., Ercoli, L., 2022. Conservation agriculture practices drive maize yield by regulating soil nutrient availability, arbuscular mycorrhizas, and plant nutrient uptake. Field Crop. Res. 277, 108403 https://doi.org/10.1016/j.fcr.2021.108403.

Mohler, C.L., 2001. Weed life history: indentifying vulnerabilities. In: Liebman, M., Mohler, C.L., Staver, C.P. (Eds.), Ecological Management of Agricultural Weeds. Cambridge University Press, Cambridge, UK, pp. 40–98.

Muoni, T., Rusinamhodzi, L., Rugare, J.T., Mabasa, S., Mangosho, E., Mupangwa, W., Thierfelder, C., 2014. Effect of herbicide application on weed flora under conservation agriculture in Zimbabwe. Crop Prot. 66, 1–7. https://doi.org/10.1016/j.cropro.2014.08.

Ngwira, A., Johnsen, F.H., Aune, J.B., Mekuria, M., Thierfelder, C., 2014. Adoption and extent of conservation agriculture practices among smallholder farmers in Malawi. J. Soil Water Conserv. 69, 107–119. https://doi.org/10.2489/jswc.69.2.107.

Nichols, V., Verhulst, N., Cox, R., Govaerts, B., 2015. Weed dynamics and conservation agriculture principles: a review. Field Crops Res. 183, 56–68. https://doi.org/10.1016/j.fcr.2015.07.012.

Nyamangara, J., Mashingaidze, N., Masvaya, E.N., Nyengerai, K., Kunzekweguta, M., Tirivavi, R., Mazvimavi, K., 2014. Weed growth and labor demand under hand-hoe based reduced tillage in smallholder farmers' fields in Zimbabwe. Agric. Ecosyst. Environ. 187, 146–154. https://doi.org/10.1016/j.agee.2013.10.005.

Oerke, E.C., 2006. Crop losses to pests. J. Agric. Sci. 144, 31–43. 〈https://doi:10.1017/S0021859605005708〉.

Pielou, E.C., 1969. An Introduction to Mathematical Ecology. Wiley-Interscience Publications, New York.

Pyšek, P., Kučera, T., Jarošík, V., 2002. Plant species richness of nature reserves: the interplay of area, climate and habitat in a central European landscape. Glob. Ecol. Biogeogr. 11, 279–289. https://doi.org/10.1046/j.1466-822X.2002.00288.x.

Pyšek, P., Jarošík, V., Kropáč, Z., Chytrý, M., Wild, J., Tichý, L., 2005. Effects of abiotic factors on species richness and cover in Central European weed communities. Agric. Ecosyst. Environ. 109, 1–8. https://doi.org/10.1016/j.agee.2005.02.018.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL 〈https://www.R-project.org/〉. Version 4.2.1. "Funny-Looking Kid."

Robinson, T.M.P., Gross, K.L., 2010. The impact of altered precipitation variability on annual weed species. Am. J. Bot. 97, 1625–1629. https://doi.org/10.3732/ajb.1000125.

Rodenburg, J., Demont, M., Zwart, S.J., Bastiaans, L., 2016. Parasitic weed incidence and related economic losses in rice in Africa. Agric. Ecosyst. Environ. 235, 306–317. https://doi.org/10.1016/j.agee.2016.10.020.

Rodenburg, J., Randrianjafizanaka, M.T., Büchi, L., Dieng, I., Andrianaivo, A.P., Ravaomanarivo, L.H.R., Autfray, P., 2020. Mixed outcomes from conservation practices on soils and Striga-affected yields of a low-input, rice–maize system in Madagascar. Agron. Sustain. Dev. 40, 1–11. https://doi.org/10.1007/s13593-020-0612-0.

Sánchez, A.M., Luzuriaga, A.L., Peralta, A.L., Escudero, A., 2014. Environmental control of germination in semi-arid Mediterranean systems: the case of annuals on gypsum soils. Seed Sci. Res. 24, 247–256. https://doi.org/10.1017/S0960258514000154.

Santín-Montanyá, M.I., Gandía, M.L., Casanova, C., Sánchez-Jiménez, F.J., Tenorio, J.L., 2020. The influence of soil tillage system on Salsola kali L. emergence during the fallow period within cereal fields. Soil Use Manag. 36, 594–603. https://doi.org/10.1111/sum.12629.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, Illinois.

Sharma, G., Shrestha, S., Kunwar, S., Tseng, T., 2021. Crop diversification for improved weed management: a review. Agriculture 11. https://doi.org/10.3390/agriculture11050461.

Silberg, T.R., Chimonyo, V.G.P., Richardson, R.B., Snapp, S.S., Renner, K., 2019. Legume diversification and weed management in African cereal-based systems. Agric. Syst. 174, 83–94. https://doi.org/10.1016/j.agsy.2019.05.004.

Storkey, J., Neve, P., 2018. What good is weed diversity. Weed Res 58, 239–243. https://doi.org/10.1111/wre.12310.

Suttle, K.B., Thomsen, M.A., Power, M.E., 2007. Species interactions reverse grassland responses to changing climate. Science 315, 640. https://doi.org/10.1126/science.1136401.

Swanton, C.J., Clements, D.R., Derksen, D.A., 1993. Weed succession under conservation tillage: a hierarchical framework for research and management. Weed Technol. 7, 286–297. https://doi.org/10.1017/S0890037X00027615.

Teasdale, J.R., Mohler, C.L., 2000. The quantitative relationship between weed emergence and the physical properties of mulches. Weed Sci. 48, 385–392. https://doi.org/10.1614/0043-1745(2000)048[0385:TQRBWE]2.0.CO;2.

Thierfelder, C., Baudron, F., Setimela, P., Nyagumbo, I., Mupangwa, W., Mhlanga, B., Lee, N., Gérard, B., 2018. Complementary practices supporting conservation agriculture in southern Africa. A review. Agron. Sustain. Dev. 38, 16. https://doi.org/10.1007/s13593-018-0492-8.

Tittonell, P., Giller, K.E., 2013. When yield gaps are poverty traps: the paradigm of ecological intensification in African smallholder agriculture. Crop Yield Gap Anal. – Ration. Methods Appl. 143, 76–90. https://doi.org/10.1016/j.fcr.2012.10.007.

Ulber, L., Steinmann, H.-H., Klimek, S., Isselstein, J., 2009. An on-farm approach to investigate the impact of diversified crop rotations on weed species richness and composition in winter wheat. Weed Res. 49, 534–543. https://doi.org/10.1111/j.1365-3180.2009.00722.x.

Zhang, J., Wu, L.-F., Li, B.-B., 2021. Weed responses to crop residues management in a summer maize cropland in the North China Plain. Agriculture 11. https://doi.org/10.3390/agriculture11080746.