



Conservation agriculture practices drive maize yield by regulating soil nutrient availability, arbuscular mycorrhizas, and plant nutrient uptake

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ABSTRACT

Conservation agriculture (CA) can sustainably increase crop productivity through improved soil chemical, physical, and biological properties, among others. However, the implementation of all its three main components (i.e., no-tillage, organic soil cover/mulch, and crop diversification) in southern Africa is often challenging, resulting in variable yield responses. Disentangling the contributions of CA practices is necessary to understand the drivers of maize grain yield within the region. Here we analysed two 6-year long component omission experiments, one at a sandy soil location and the other at a clay soil location. In these two experiments, soil chemical parameters, total plant nutrient uptake, rate of crop residue decomposition, and arbuscular mycorrhizal fungi (AMF) colonization of maize roots were assessed. Soil chemical properties only differed across systems at the sandy soil location with the mulched systems under no-tillage (NT) resulting in increased soil organic carbon levels, total nitrogen, and soil available phosphorus as compared to conventional tillage with no mulch or rotation (CT). Conventional tillage-based systems resulted in fastest decomposition of maize residues, while systems with NT and rotation resulted in highest AM fungal root colonization rate of maize at the clay soil location. Total plant N uptake was almost 2-fold higher in tilled and no-tilled systems with both mulch (M) and rotations (R) (i.e., NT+M+R and CT+M+R) as compared to CT. Structural equation modeling was used to disentangle the links between cropping systems, soil chemical and biological properties, plant nutrient uptake, and maize grain yield. Cropping systems had direct and indirect influences on yield at both locations. At both locations, cropping systems influenced yield via plant N uptake, with the NT+M+R and CT+M+R systems having more beneficial effects compared to other systems, as shown by their higher path coefficients. In conclusion, we recommend a more holistic approach to cropping system assessment that includes a higher number of abiotic and biotic determinants. This would allow for a more rigorous evaluation of the drivers of yield and increase our understanding of the effects and performance of practices under the prevailing agro-ecological conditions.

1. Introduction

Agroecosystem functions, such as crop production and nutrient cycling, are mainly driven by agricultural practices and these effects may either be direct or indirect. The direct effect is determined by the implementation of the agricultural management practices into the cropping system (i.e., the type and distribution in time and space of crops and the level of management and utilized resources; Conway, 1987). Thus, the analysis of the effect of cropping systems on yield should apply a holistic approach which considers it as a functional unit, similar to the plant genotype, directly influencing productivity. The

indirect effects of agricultural practices can arise from the changes in key soil chemical properties, such as carbon (C) and nitrogen (N) content (Smith et al., 2016) amongst other essential plant nutrients. For example, deep plowing and residue removal have been shown to be the major drivers of soil organic C (SOC) decomposition (Morari et al., 2006). Under conventional tillage systems, the mineralization of C and N is enhanced through the incorporation of crop residues and other organic material, but in such systems soil aggregates are disrupted, resulting in a poor organic matter build-up (Hazarika et al., 2009; Piazza et al., 2020). Moreover, in such systems, other soil properties such as water infiltration and aeration are diminished over time (Thierfelder

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and Wall, 2010).

In southern Africa, many smallholder farmers mainly rely on soil inversion using mouldboard plows at the beginning of the season to control weeds (Lee and Thierfelder, 2017). While this provides a fine soil tilth and improve aeration, this practice leads to the breakdown of soil aggregates, resulting in poor soil stability and hence high risk of accelerated erosion (Thierfelder et al., 2014). Significant amounts of nutrients are lost from agricultural fields through soil erosion; for example, in a study carried out in Zimbabwe, Munodawafa (2012) showed that under plow-based conventional tillage systems, about 23 kg N ha⁻¹ year⁻¹ is lost. Thus, many smallholder farming systems are characterized by poor yield, leading to poor nutrition and large yield gaps (Henderson et al., 2016; Mwila et al., 2021). In developed countries, yield gaps are mitigated mainly with the application and reliance on synthetic fertilizers (Pradhan et al., 2015). Although chemical fertilizer use, particularly N, phosphorus (P), and potassium (K), has recently increased in developing countries, in southern Africa the use of mineral fertilizers is limited by different aspects, such as unfavorable abiotic (e.g., low rainfall) and economic (e.g., unaffordability and inaccessibility) conditions (Ryan et al., 2013). Moreover, micronutrients such as iron (Fe), copper (Cu), manganese (Mn), zinc (Zn), which are essential for healthy growth, development, and reproduction of higher plants (White and Brown, 2010), are also often neglected by smallholder farmers.

In view of the low input use in smallholder farming systems, there is need to implement cropping systems aiming at improving soil physical and biological properties, nutrient stocks, and crop nutrient uptake, while being economical and sustainable. Based on previous research, conservation agriculture (CA) is potentially one of these systems. Long-term implementation of CA has demonstrated to improve soil water properties, SOC, and hence crop yield in soils with low SOC (De Sanctis et al., 2012; Mhlanga et al., 2021a). Conservation agriculture is defined as a system that combines the use of reduced or no-tillage (NT) with soil cover through mulching with crop residues, and diversified crop species including legumes (FAO, 2019) amongst other complimentary practices (Thierfelder et al., 2018). Soil biological properties, such as enzymatic activities, microbial abundance as well as community structure, have been shown to be shaped by management practices and to be improved under NT or reduced tillage based systems (Choudhary et al., 2018; Piazza et al., 2019, 2020). Within plant beneficial microbes, arbuscular mycorrhizas (AM) are symbiotic associations established between soil-borne fungi (Glomeromycotina; Spatafora et al., 2016) and the roots of most crops, including maize (*Zea mays* L.). AM fungi play a fundamental role in soil fertility and plant nutrition, improving the crop ability to take up nutrients, such as P, N, and micronutrients (e.g., Fe and Zn) from the soil through the extraradical mycelial network, and thus potentially improving yield (Hu et al., 2009; Pellegrino et al., 2015; Cardini et al., 2021). In return, the plant supplies AM fungi with photosynthetically fixed carbohydrates via intracellular structures called arbuscules (Bago et al., 2000; Schüßler et al., 2006). No-tillage systems have a positive effect on AM fungal diversity, spore number, and density of AM fungal hyphae that increase the infection potential of soil and boost the AM fungal colonization of roots (Jansa et al., 2002; Helgason et al., 2010). This results in yield increases and enhanced glomalin concentration (Borie et al., 2006) with implications for soil stability (Bedini et al., 2009).

Despite the evidence of the positive impacts of CA, southern African smallholder farmers are facing many socio-economic challenges hampering the implementation of all its three components (Ward et al., 2018). This has resulted in variable yield responses to CA practices across the region. A recent study by Mhlanga et al. (2021a) showed that yield response is variable with varying degrees of implementation of the CA components, but mulching is crucial in stabilizing yields in the short- to medium-term across different environments in the region. Furthermore, the study showed that overall, the implementation of crop rotations and mulching either in NT or conventional tillage systems resulted in comparable productivity. Therefore, to clarify the role of mulch on

the underlying drivers of yield responses, it is necessary to dissect the complexity of nutrient release and plant uptake pathways under contrasting conditions of soil texture and organic matter turnover.

The overall aim of this study was to provide empirical evidence for the response of maize grain yield to the combined effects of cropping systems and soil parameters, such as SOC, total N, available P, soil pH; plant nutrient uptake; arbuscular mycorrhizal fungal root colonization of maize; and rate of decomposition of the crop residues. We hypothesized that the different combinations of CA involving mulching (i) are more effective in organic matter build-up and improvement of soil chemical properties; (ii) increase plant nutrient uptake; and (iii) promote the establishment of an effective symbiosis with AM fungi. Moreover, we hypothesized that the response to CA would be strongest in sandy soil, in which organic matter is lower and yield response is more dependent on residue decomposition. To overcome the challenges in determining the response of grain yield to environmental factors that covary across space and time in agricultural soils, we selected two of the eight experiments from the work of Mhlanga et al. (2021a) with contrasting soil texture (sandy and clay) including eight cross-factorial combinations of no-tillage, rotation, and mulching. These selected experiments had equal length of experimentation (six years) suggesting a stable state of cropping system effects. We determined soil chemical parameters (namely, SOC, total N, available P, and pH), plant nutrient uptake of micro- and macro- elements, and AM fungal root colonization of maize at both locations. Following our hypothesis, the rate of decomposition of crop residues was only assessed at the sandy location. We then used the path analysis to distinguish between direct and indirect drivers of grain yield.

2. Material and methods

2.1. Experimental field location

The experiment was initiated in the summer growing season of 2013–14 at two locations: Domboshawa Training Center (DTC) (latitude 17.62° S; longitude 31.17° E; and altitude of 1560 m asl) and University of Zimbabwe (UZ) (latitude 17.73° S; longitude 31.02° E; and altitude of 1503 m asl). The data presented here were collected in the growing season 2018–2019. Soil characteristics in this year are therefore a result of 6 years of previous treatment. The soil at the DTC location has clay, sand, and silt contents of 220 g kg⁻¹, 730 g kg⁻¹, and 50 g kg⁻¹ and organic carbon (C) content of 7.3 g kg⁻¹ and is classified as *Arenosols* (IUSS Working Group, 2015) (hereafter called sandy location). The soil at UZ has 400 g kg⁻¹ clay, 390 g kg⁻¹ sand, and 210 g kg⁻¹ silt, and a C content of 16.8 g kg⁻¹ and classified as *Rhodic Lixisols* (hereafter called clay location). According to the Köppen–Geiger classification, the climate of the locations is classified as warm temperate with dry winters and hot summers (Cwa) (Kottek et al., 2006). Long-term average (10-year) annual maximum and minimum temperatures are 31 °C and 10 °C, respectively for both DTC and UZ locations. The long-term average annual rainfall at the DTC and UZ are 814 mm and 826 mm, respectively. During the 2018–19 season, both locations received below-average total annual rainfall: 603 mm at DTC and only 383 mm at UZ (Fig. 1). The sites also experienced mid-season dry spells of up to 20 days.

The mean seasonal maximum air temperatures were 29.0 °C and 27.5 °C at DTC and UZ, respectively, while the mean air minimum temperatures were 15.1 °C at both sites.

2.2. Experimental set-up and crop management

The experiments were set up in a randomized complete block design (RCBD) with eight treatments (hereafter referred to as cropping systems) replicated four times:

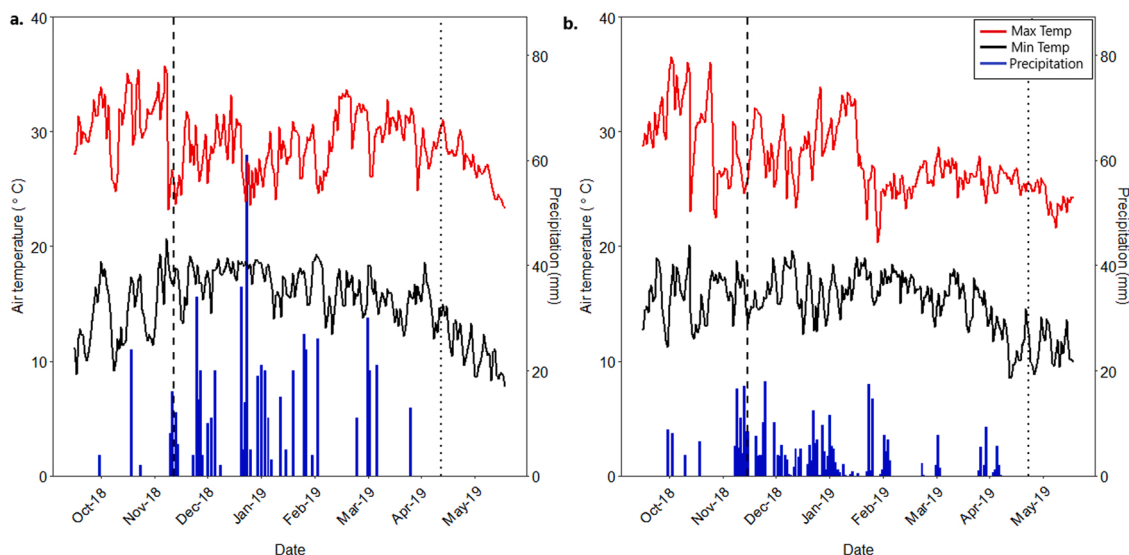


Fig. 1. Daily air maximum temperature (Max Temp), air minimum temperature (Min Temp), and precipitation at (a) Domboshawa Training Center (sand location) and at (b) University of Zimbabwe (clay location) during the 2018–19 crop growing season. The dashed vertical lines signify the sowing dates while the dotted vertical lines signify the harvesting date.

- i. Conventional tillage (CT) – land preparation was done through digging with a hand hoe to simulate plowing and maize was sown as a sole crop in riplines that were created afterwards using an animal-drawn Magoye ripper (a traditional plow with the mouldboard replaced with a ripper tine) at DTC and in basins created using a hand hoe at UZ. All crop residues were removed after harvesting.
- ii. Conventional tillage plus mulch (CT+M) – land preparation and maize sowing were done as in the CT treatment, but crop residues were retained on the soil surface for cover at planting at a rate of 2.5 t ha⁻¹.
- iii. Conventional tillage plus rotation (CT+R) – land preparation was done as in the CT treatment and maize was rotated with cowpea (*Vigna unguiculata* L.). All crop residues were removed after harvesting.
- iv. Conventional tillage plus mulch and rotation (CT+M+R) – land preparation was done as in the CT treatment and maize was rotated with cowpea. Crop residues were retained on the soil surface for cover at planting at a rate of 2.5 t ha⁻¹.
- v. No-tillage (NT) – Sole maize was sown in riplines created using an animal-drawn Magoye ripper (no further soil disturbance was done) at DTC and in basins created using a hand hoe at UZ. All crop residues were removed after harvesting.
- vi. No-tillage plus mulch (NT+M) – Maize was sown as in the NT treatment and crop residues were retained on the soil surface for cover at planting at a rate of 2.5 t ha⁻¹.
- vii. No-tillage plus rotation (NT+R) – Maize was sown in riplines and rotated with cowpea. All crop residues were removed after harvesting.
- viii. No-tillage plus mulch and rotation (NT+M+R) – Maize was sown in riplines and rotated with cowpea and crop residues were retained on the soil surface for cover at planting at a rate of 2.5 t ha⁻¹.

The treatments were established in plots measuring 12 m × 6 m (72 m²). For the treatments that involved rotation, the plots were split. Maize was sown on one side of the plot while cowpea on the other side, such that maize and cowpea yield were represented in each year and then switched every alternate year. 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. Sowing of crops was done after receiving the first effective rainfall which was determined by receiving at least 30 mm of rain within two days after the beginning of November (Fig. 1). At sowing (which was done on the 26th of November 2018 at DTC and 29th of November 2018 at UZ) (Fig. 1), both maize and cowpea received a basal fertilizer at the rate of 11.6 kg N ha⁻¹, 10.1 kg P ha⁻¹, 9.6 kg K ha⁻¹. Maize further received a top-dressing fertilizer in the form of ammonium nitrate at 23 kg N ha⁻¹ applied at four and seven weeks after sowing. No top-dressing was applied to the rotated cowpea. Immediately after sowing, weeds were controlled by spraying glyphosate [*N*-(phosphono-methyl) glycine], as a pre-emergent herbicide, at the rate of 1.025 L active ingredient ha⁻¹. This was followed by manual hoe weeding whenever weeds were 10 cm tall or 10 cm in diameter for stoloniferous weeds.

2.3. Effect of cropping systems on soil nutrient availability and content

Four soil samples were randomly collected from each plot in November 2018, prior to the beginning of the season (before beginning of rainfall, after the long-dry off-season period; called pre-season, hereafter), and at the R1 growth stage of maize (when 75% of plants had silks visible and pollen shading; called R1, hereafter) (Pannar, 2016). The soil samples were collected next to four tagged plants in the row space to a depth of 10 cm and mixed to make a composite sample for each plot. These four plants were randomly chosen and tagged to be sampled for further analyses on AM fungal root colonization and nutrient uptake. Since soil sampling should not occur close to soil management practices, it was performed before the first effective rain (Alef and Nannipieri, 1995). Indeed, the region in which the experiments were conducted experiences long dry winter periods in-between crop growing seasons, that is, from April to November. Thus, the fact that we sampled the soil in November after five years of CA implementation and just after the first effective rain allowed to investigate the long-term cropping system effect on soil properties. Indeed, temporal variability of soil properties have been shown to be fairly stable and to marginally change during the cropping season in several climatic conditions, including the study area (Laamrani et al., 2020). Moreover, we could also investigate the long-term cropping system effect on biological parameters, such as AM fungi, because they have been shown to consistently maintain the same patterns of variability among different cropping systems, although they can change among and within the

seasons (Pellegrino et al., 2015). For this reason, we decided to also sample soil parameters together with the biological parameters at the R1 stage which is a critical maize growth stage. At the R1 stage, maize is sensitive, and stress can cause abortion of kernels and N and P uptake by the crops is still rapid. The plant also begins to translocate nutrients from other plant parts to the cob (Pannar, 2016). Moreover, the soil would have a relatively stable response to the seasonal rains and it was humid enough for AM fungal proliferation (Oehl et al., 2003).

Soil samples were air-dried and sieved through a 2 mm mesh and analysed for soil organic carbon (SOC) (Walkley-Black wet combustion method; Nelson and Sommers, 1982), total N (TN) (macro Kjeldahl digestion procedure; Bremner and Mulvaney, 1982), and available phosphorus (P_{avail}) (Olsen method using a solution of sodium bicarbonate; Olsen and Sommers, 1982) and pH (potentiometric method in 1:2.5 (soil:water); McLean, 1982). Bulk density of the soil (only for samples collected at pre-season) was measured using the Blake and Hartge method (Blake and Hartge, 1986). Soil TN and SOC contents (in t ha^{-1}) were expressed as a product of bulk density and the concentration of the elements in the soil (0–10 cm soil depth).

2.4. Effect of cropping systems on total plant nutrient uptake and maize yield

At physiological maturity (R6; Pannar, 2016), grain and stover (stalk plus leaves) were collected from the four tagged plants and mixed to make a composite sample per plot. All plant material collected were air-dried until constant weight and milled through a 2 mm sieve using an IKA® microfine grinder drive (IKA-Werke, Germany). Approximately 0.3 g of plant material was weighed and digested using a microwave digester (Coolpex Smart Microwave Reaction System, PreeKem, Harthausen, Germany) with 8 ml of 69% HNO_3 and analysed for micro-nutrients (zinc, Zn; copper, Cu; iron, Fe; magnesium, Mg; manganese, Mn; calcium, Ca; potassium, K) by Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) using an Agilent SPS 4 autosampler spectrometer (Agilent, CA, United States). Nitrogen and P concentrations in grain and stover were determined by the Kjeldahl method and the ammonium-molybdophosphoric blue color method, respectively (Townes, 1986). For grain yield assessment, maize plants were harvested from each plot (including the four tagged plants) from an area of 18 m^2 ($5 \text{ m} \times 3.6 \text{ m}$).

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. Grain moisture content was determined, and yield was expressed at 12.5% moisture content. Maize stover was determined on a dry weight basis. Yield data were calculated per unit of surface area (ha). Total plant nutrient uptake (TPNU) was calculated using grain yield and stover and their nutrient concentrations as at the R6 stage using the formula:

$$\text{TPNU (kg ha}^{-1}\text{)} = [\text{grain nutrient concentration (mg kg}^{-1}\text{)} \times \text{grain yield (t ha}^{-1}\text{)}] + [\text{stover nutrient concentration (mg kg}^{-1}\text{)} \times \text{stover yield (t ha}^{-1}\text{)}].$$

2.5. Effect of cropping systems on AM fungal root colonization of maize

For the assessment of AM fungal root colonization, maize roots were collected from the four tagged plants in each plot at R1 stage. One quarter of the root system of each plant was collected by digging with a hand hoe without uprooting the whole plant and were mixed to form one composite sample per plot. The roots were immediately washed to remove soil under running tap water and fine roots were selected, air-dried, and stored at 4°C before staining. The roots were cleared in 10% KOH solution at 90°C for 45 min, acidified in HCl 1% for 1 h and stained with 0.05% Trypan blue, using lactic acid instead of phenol (Phillips and Hayman, 1970), at 90°C for 30 min, and the percentage of colonization was assessed using the magnified intersections method of McGonigle et al. (1990) ($200 \times$ magnification). Roots from each

replicate were cut into pieces 1 cm long and about 20 roots were mounted on each microscope slide using acidic glycerol (1% HCl plus glycerol, 1:1 v/v) and each slide was inspected to have a total of 100 intersections per slide.

2.6. Effects of cropping systems on maize residue decomposition

The rate of maize residue decomposition in the different cropping systems was assessed using the litterbag method at the sandy location. Litterbags were constructed using nylon mesh of different mesh size i.e., 5 mm (referred to as course mesh hereafter – 06-5000/72 SEFAR NITEX, Torino, Italy) and $41 \mu\text{m}$ (fine mesh – 03-41/31 SEFAR NITEX, Torino, Italy) and all litterbags had a dimension of $20 \times 20 \text{ cm}$. Each litterbag was filled with 50 g of maize residues collected from the experimental area. Course mesh allowed all microorganisms access to the litter, while the fine mesh excluded larger organisms but allowed only bacteria and fungi (Luan et al., 2020). Five litterbags of each mesh size were placed in each plot immediately after maize emergence and were collected on 30-day intervals (5 times during maize crop growth cycle). In conventional tillage-based plots, litterbags were buried in the soil to a depth of 10 cm to simulate plowing-in of crop residues, while in no-tillage-based treatments, litterbags were placed on the surface and held in place using lawn staples to ensure contact with the soil. After each collection, litterbag contents were cleaned of soil, fresh weight was measured and then they were oven-dried for 72 h at 80°C until constant weight.

2.7. Statistical analyses

The effect of the cropping systems on soil chemical parameters, TPNU, and AM fungal root colonization was analysed separately for each location. Moreover, the effect of cropping system, time of field exposure, and their interaction on litterbag weights was analyzed separately for each mesh size. The normality of the model residuals and the homoscedasticity of the variance residuals were checked and, where necessary, data were $\log(\times + 1)$ -transformed except for AM fungal colonization data which were square root-arcsine-degrees transformed before analysis of variance (ANOVA). Back-transformed data means are reported. Analyses were done using mixed modeling procedures in R environment (R Core Team, 2021). Model selection was carried out based on the Akaike Information Criterion (AIC) and in the most suitable model, cropping system was regarded as fixed factor, while block was regarded as random factor. For the litterbag weight data, number of days of litterbag field exposure was also included in the model as a fixed factor. The significance of the cropping system was estimated by F-tests using the 'lme4' package in R (Bates et al., 2015). Where means significantly differed, multiple comparisons based on post-hoc Tukey tests, were done using the 'emmeans' package in R (Lenth, 2019). To assess the relationship between the cropping systems (explanatory variables) and response variables (soil chemical parameter, TPNU, AM fungal colonization and residue decomposition rate), a redundancy analysis (RDA) was used in CANOCO 5 (Lepš and Šmilauer, 2014). Since response data were not compositional, it was more appropriate to carry out a constrained linear response-based ordination analyses, hence RDA. In the analyses, response variables were centered, and standardized and unrestricted Monte Carlo permutational tests were run (set at 999 permutations) for the determination of statistical significance of the relationship.

To assess the interactions between cropping systems, TPNU, soil chemical properties, AM fungal root colonization, residue decomposition rate, and maize grain yield, we used a mixed model structural equation modeling (SEM) for each soil type using the 'pairwiseSEM' (Lefcheck, 2016) and 'nlme' (Pinheiro et al., 2019) packages in R. The models were based on hypothetical pathways and were fit and evaluated using restricted maximum likelihood. In the models, the parameters were maize grain yield; total N, P, and K uptake (as measures of total plant nutrient uptake); SOC, soil TN, and soil P_{avail} (as measures of the

soil chemical properties, considering soil samples collected at the R1 stage); AM fungal root colonization; and rate of residue mass loss (as a measure of residue decomposition using the 5 mm mesh data as this reflected more accurate decomposition). Although micronutrients are important, their results were insignificant, and reduced the fit of the models, and were therefore omitted in this modeling. Blocks were included in the models as a random factor. In the pathway, we allowed cropping systems to directly affect maize grain yield and indirectly affect it through the other measured parameters mentioned above. We assumed that soil TN and SOC are being driven by an underlying driver and hence we estimated their covariance. Since cropping system was a categorical variable, the evaluation of its influence on other variables was done using tests of directed separation for individual model pieces (Lefcheck, 2016). Thus, the estimated standardized path coefficients (λ) for the proximate and ultimate pathways are reported. We compared individual cropping systems effects using post-hoc means adjusted Tukey tests (Lenth, 2019).

3. Results

3.1. Effect of CA cropping systems on soil chemical properties

At pre-season, SOC, TN, P_{avail} , were significantly different across the cropping systems only at the sandy location, whereas soil pH was not affected (Table 1). The NT+M system had the highest soil TN which was 50% higher compared to CT and CT+R systems (1.1 t ha^{-1} vs. 0.7 t ha^{-1}) (Fig. 2a). At the sandy site, the NT+M system also resulted in the highest SOC, averaging 11.6 t ha^{-1} , whereas the lowest contents were observed under CT+R and NT+R systems (8.9 t ha^{-1} on average), although these systems were comparable with CT and NT systems (Fig. 2b).

Available P was the highest under the NT+M system (83.8 mg kg^{-1}) which was almost double compared with the CT+M and CT systems (Fig. 2c). At the sandy site and at R1 stage, SOC, TN, P_{avail} , and pH were also consistently different across the systems, while at the clay site only P_{avail} differed across the systems (Table 1). At the sandy site, TN was 41% higher under the CT+M system than under the NT+R system, which showed the lowest TN (Fig. 2e). Soil organic C was the highest under the CT+M and NT+M systems, which averaged 10.6 t ha^{-1} and the lowest under the NT+M and NT+M+R systems (Fig. 2f). The CT+M+R system had the highest concentration of P_{avail} (79 mg kg^{-1}), while CT, CT+M, CT+R, NT, and NT+R had the lowest P_{avail} (Fig. 2g).

Soil pH was also the highest under CT+M+R system, with a value of 5.3 as compared to 4.9 in the NT system (Fig. 2h). At the clay location,

adding mulch either to NT or conventional tillage, or practising CT resulted in the highest P_{avail} concentrations, averaging 62.1 mg kg^{-1} (Fig. 2i).

3.2. Effect of cropping systems on plant nutrient uptake and yield

At the sandy location, only the uptake of Zn was significantly affected by the cropping systems (Table 2). The CT+M+R system resulted in the highest Zn uptake, averaging 0.3 kg ha^{-1} , while maize grown under CT showed the lowest Zn uptake (Table 2). Although the differences were marginal, NT+M resulted in a considerably higher P uptake.

At the clay location, the uptake of N, P, and Zn significantly differed across the cropping systems (Table 2). The use of all three components (NT+M+R) resulted in the highest N uptake which was 72% more than that under the CT system (Table 2). On the other hand, the CT+M, CT+R, and NT+M systems resulted in the highest uptake of P, averaging 11.2 kg ha^{-1} (Table 2). The CT system also resulted in the lowest P uptake. The NT+M+R system showed the highest Zn uptake, which was 59% higher than under the CT system, showing the lowest uptake.

At the sandy location, both maize grain yield and stover did not differ across the cropping systems (Table 2). At the UZ location, both grain yield and biomass significantly differed between the cropping systems. The NT+M+R and the CT+M+R systems resulted in the highest grain yield, averaging 3.5 t ha^{-1} , while the CT system showed the lowest yield (Table 2). On the other hand, the NT+M+R attained the highest stover (Table 2).

3.3. Effect of cropping systems on AM fungal root colonization of maize

At the sandy location, cropping systems did not affect AM fungal root colonization or the percentage of arbuscules and vesicles (Figs. 3a and 3b). Conversely, at the clay location, cropping systems significantly affected AM fungal root colonization as well as percentage of vesicles. The NT+R (65.2%), NT+M+R (58%), and CT+M+R (53%) systems had the highest AM fungal root colonization as compared with CT, NT+M, and CT+M systems, averaging 42% (Fig. 3c). Almost similar trends were also observed for vesicles with the NT+R (12%) and NT+M+R (7%) systems having the highest percentages, while CT and NT systems having the lowest values (Fig. 3d).

3.4. Effects of cropping systems on maize residue decomposition

For both mesh sizes, litterbag weights (percentage of initial mass)

Table 1

Effect of cropping systems on soil chemical properties measured before the beginning of the season (preseason) and during the anthesis-silking stage of maize (R1 stage) in the 2018–19 season at Domboshawa Training Center (sand location) and at University of Zimbabwe (clay location).

Location	Period sample collected	Chemical properties	Sum of squares	Mean square	DF	F-value [†]
Domboshawa Training Center	Preseason	Total nitrogen	0.53	0.08	7	5.21 **
		Organic carbon	48.10	6.87	7	3.09 *
		Available phosphorus	5312.80	758.98	7	5.03 **
		pH	2.85	0.41	7	2.27.
	R1 stage	Total nitrogen	0.33	0.05	7	3.08 **
		Organic carbon	83.08	11.87	7	6.96 ***
		Available phosphorus	152.94	21.85	7	0.35 ns
		pH	0.58	0.08	7	3.23 *
University of Zimbabwe	Preseason	Total nitrogen	0.149	0.02	7	1.02 ns
		Organic carbon	28.8	4.10	7	1.14 ns
		Available phosphorus	611.74	87.39	7	0.40 ns
		pH	0.080	0.01	7	0.47 ns
	R1 stage	Total nitrogen	0.10	0.00	7	1.08 ns
		Organic carbon	33.10	4.70	7	1.28 ns
		Available phosphorus	5312.80	759.00	7	5.03 **
		pH	0.10	0.00	7	1.76 ns

[†] Asterisks show the significance level: ***, ** and * represent $P < 0.001$, < 0.01 and < 0.05 , respectively; and ns means not significant; and ‘.’ represent marginally significant.

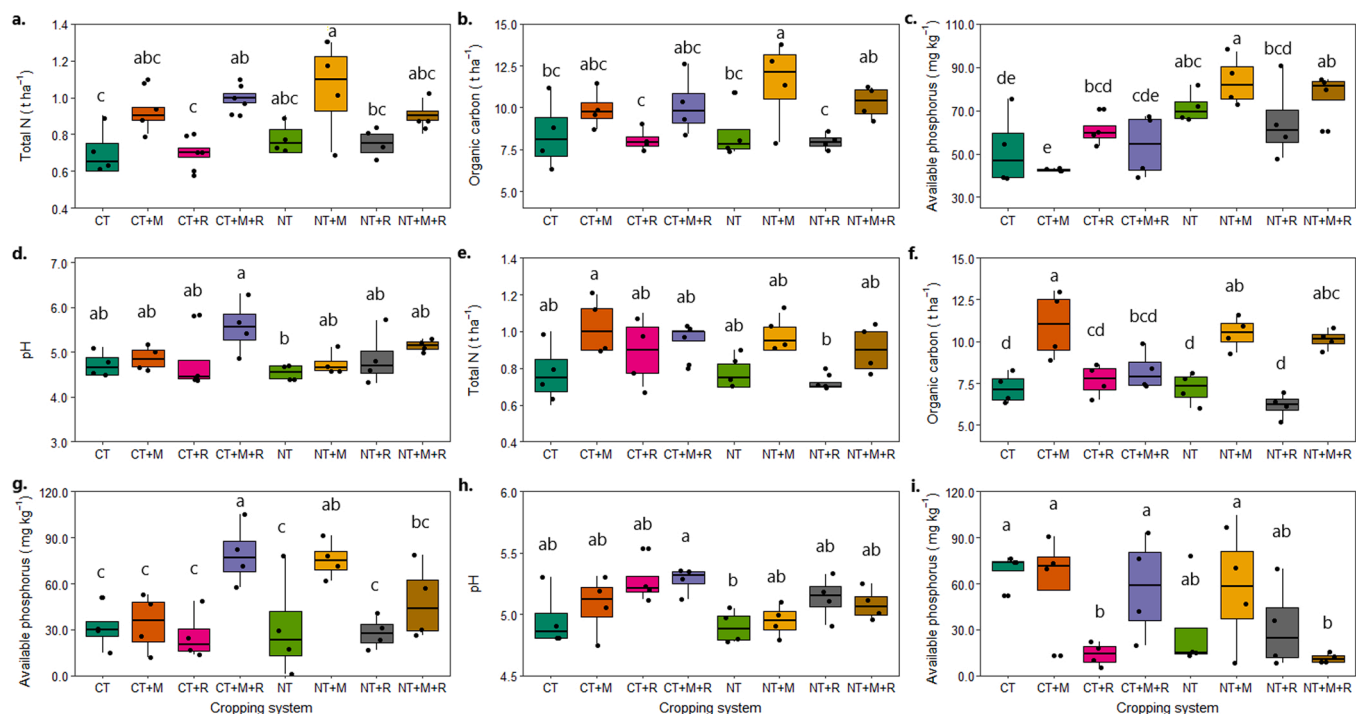


Fig. 2. Effect of cropping systems on soil total nitrogen (N) (a and e), soil organic carbon (b and f), soil available phosphorus (c, g and i), and pH (d and h) of soil collected before the start of the season (preseason) (a to d) and at silking stage of maize (R1 stage) (e to h) at Domboshawa Training Center (sandy location); and on available phosphorus (i) at R1 stage at the University of Zimbabwe (clay location). Means of boxplots with different letters are significantly different from each other at 0.05 probability level. Each individual dot represents an observation recorded from each plot.

Table 2

Plant nutrient uptake, maize grain yield and stover as affected by the cropping systems at the Domboshawa Training Center (sandy location) and at University of Zimbabwe (clay location).

Location	Cropping system	Nutrient uptake (kg ha ⁻¹)			Grain yield (t ha ⁻¹)	Stover (t ha ⁻¹)
		Nitrogen	Phosphorus	Zinc		
Domboshawa Training Center	CT	44.80 a	7.64 a	0.12c	3.17 a	1.94 a
	CT+M	50.31 a	9.71 a	0.16 bc	3.16 a	2.75 a
	CT+R	53.62 a	10.71 a	0.19 abc	3.45 a	3.23 a
	CT+M+R	85.00 a	16.83 a	0.25 a	5.76 a	3.88 a
	NT	46.43 a	7.59 a	0.13 bc	2.81 a	2.46 a
	NT+M	60.22 a	11.28 a	0.18 abc	3.74 a	2.79 a
	NT+R	56.91 a	10.02 a	0.15 bc	3.43 a	2.34 a
	NT+M+R	73.42 a	12.51 a	0.21 ab	4.64 a	2.82 a
	<i>F-value</i> [‡]	1.83 ns	2.28 ns	2.45 *	1.60 ns	1.56 ns
University of Zimbabwe	CT	42.51 e	5.00 d	0.22 d	2.42c	3.05 e
	CT+M	61.52 bc	11.11 a	0.26 bcd	3.03 abc	4.29 abc
	CT+R	63.11 b	11.34 a	0.27 bc	3.22 ab	3.93 bcd
	CT+M+R	63.83 ab	8.51 bc	0.26 bcd	3.48 a	4.31 abc
	NT	50.64 de	5.06 d	0.24 cd	2.61 bc	3.47 de
	NT+M	52.43 cd	10.37 a	0.26 bcd	3.07 abc	4.49 ab
	NT+R	55.95 bcd	10.22 ab	0.29 b	2.98 abc	3.77 cd
	NT+M+R	73.00 a	7.08c	0.35 a	3.65 a	4.82 a
	<i>F-value</i> [‡]	8.68 ***	17.05 ***	4.28 **	2.56 *	5.85 ***

[‡] Asterisks show the significance level: ***, ** and * represent $P < 0.001$, < 0.01 and < 0.05 , respectively; and ns means not significant.

differed among the cropping systems and among the sampling periods (Fig. 4). However, the interactions between cropping system and sampling period were not significant for both mesh sizes. For the course mesh, the lowest litterbag weight (that reflects the fastest rate of decomposition), was observed under the CT+R systems, while the NT+M and NT+M+R systems had the slowest decomposition rate (Fig. 4a). In general, the CT-based systems showed higher rates of decomposition (average 61% remaining mass) as compared with the NT-based ones (average 68% remaining mass). For the fine mesh, the CT, CT+M+R, and NT systems showed the fastest decomposition rate with an average of 57.9% remaining mass compared to the NT+M and

NT+M+R systems with an average of 73.1% (Fig. 4b). As expected, a progressive decline in weight with time was reported for both mesh sizes and the course mesh size showed a steeper slope compared with the fine mesh size litterbags (Fig. 4c, d).

3.5. Linkages between cropping systems, soil chemical properties, plant nutrient uptake, AM fungal root colonization, maize residue decomposition, and yield

At the sandy location, the redundancy analysis (RDA) showed that cropping system explained 24.5% (I and II axes) of the whole variance

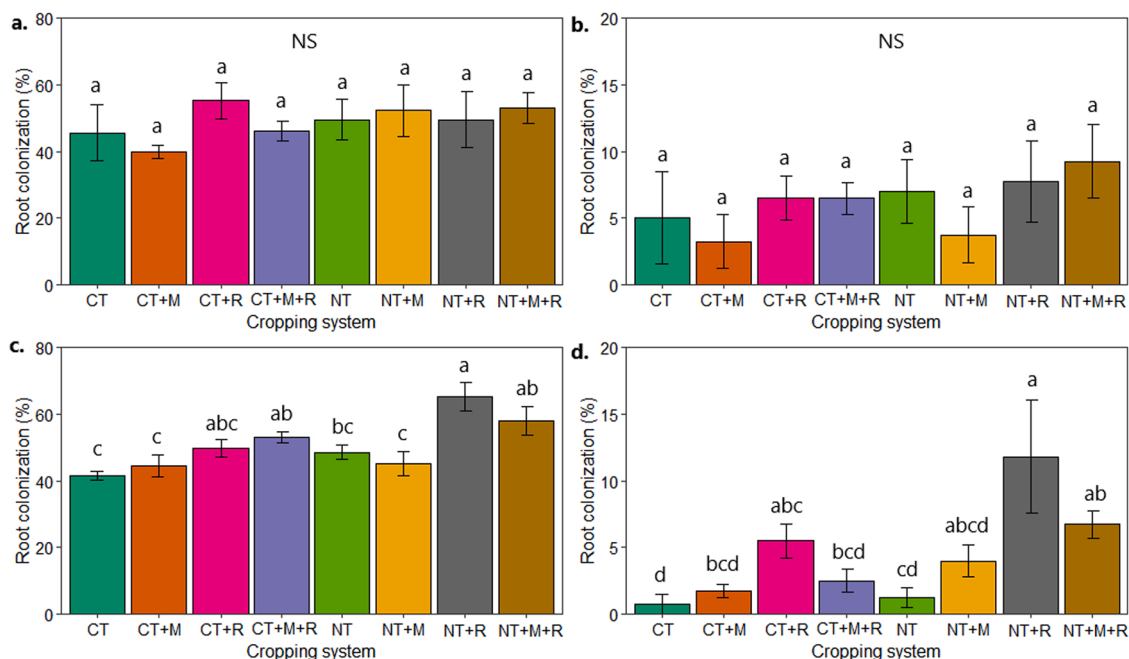


Fig. 3. Arbuscular mycorrhizal (AM) fungal root colonization of maize measured as percentage of colonized root (a), and of vesicles (b) at Domboshawa Training Center (sandy location), and as percentage of colonized root (c) and vesicles (d) at University of Zimbabwe. The roots were collected during the silking growth stage of the maize (R1 stage). Means with different letters are significantly different from each other at 0.05 probability level. The error bars represent the standard error of the mean.

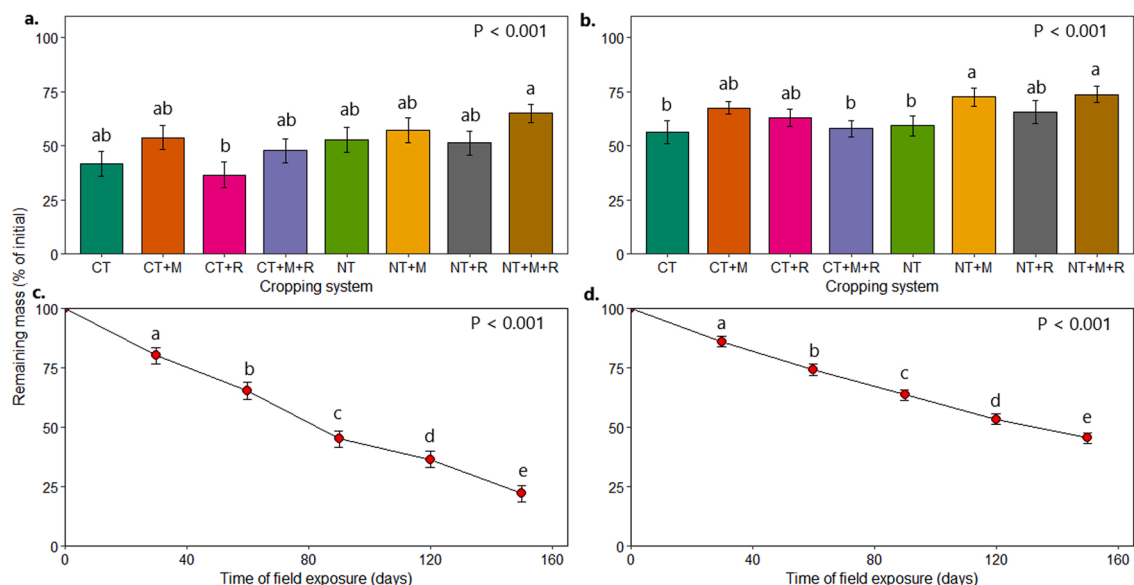


Fig. 4. Effects of different cropping systems on weight loss of litterbags containing maize crop residues for course mesh (5 mm) (a), and fine mesh (4 μm) (b); and progressive loss of weight from litterbags exposed in the field for 150 days and collected at 30-day intervals for course mesh (5 mm) (c), and fine mesh (4 μm) (d) at the Domboshawa Training Center (sandy location)..

and that its effect on the whole response variables was significant ($F = 1.9, P = 0.003$) (Fig. 5a). In detail, the Monte-Carlo permutation test showed that CT+M+R was significantly different from all the other treatments ($P = 0.042$), and that NT+M and NT+M+R were different from the other treatments as well ($P = 0.050$ and $P = 0.045$, respectively). The addition of mulch and rotation either to CT or NT was associated with higher total uptake of macro- and micronutrients by maize, higher yield, and AM fungal root colonization/vesicles (Fig. 5a). On the other hand, the addition of mulch to NT was associated with higher values of SOC and soil TN at both sampling times, and with

higher percentage of arbuscules within maize roots. The biplots also show that nutrient uptake of different nutrients were the most discriminating variables along the first axis, and thus separating CT+M+R from NT+M+R, whereas SOC was the most discriminating variable on the second axis and thus separating NT+M from full implementation and CT+M+R (Fig. 5a). At the clay location, the RDA showed that cropping system explained 25.5% (I and II axes) of the whole variance and that its effect on the whole response variables was significant ($F = 2.1, P = 0.001$) (Fig. 5b). In detail, the Monte-Carlo permutation test showed that CT and NT were significantly different

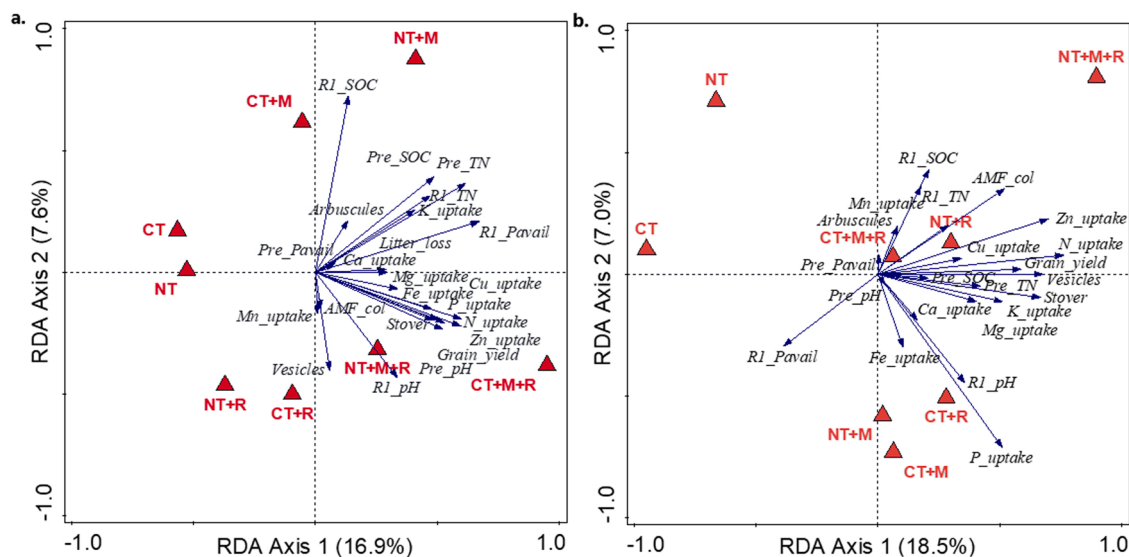


Fig. 5. Redundancy analysis of the relationship between cropping systems and plant uptake of calcium (Ca), copper (Cu), iron (Fe), potassium (K), manganese (Mn), magnesium (Mg), phosphorus (P), nitrogen (N), zinc (Zn); pre-season (Pre) soil total nitrogen (Pre_TN), soil organic carbon (Pre_SOC), available phosphorus (Pre_Pavail), pH (Pre_pH); R1 stage (R1) soil total nitrogen (R1_TN), soil organic carbon (R1_SOC), available phosphorus (R1_Pavail), pH (R1_pH); decomposition rate measured in 5 mm mesh litterbags (litter_loss); AM fungal percentage root colonization of maize (AMF_col), vesicles and arbuscules; and maize grain yield (grain_yield) and maize biomass (biomass) at Domboshawa Training Center (sandy location) (a) and at University of Zimbabwe (clay location) (b).

from all the other treatments ($P = 0.003$ and $P = 0.001$, respectively), and that NT+M+R and NT+R were different from the other treatments as well ($P = 0.018$ and $P = 0.037$, respectively). The CT and NT systems were clearly associated with low values of all the studied variables, whereas NT+M+R and NT+R were associated with higher N, Cu, Mn, and Zn uptakes, AM fungal root colonization and SOC (Fig. 5b). The diagrams point out correlations between almost all parameters (Fig. 5).

The fitness indices of the structural equation modeling (SEM) were significant at both locations (DTC: Fisher's $C = 23.0$, $P = 0.29$, $df = 20$; UZ: Fisher's $C = 15.7$, $P = 0.48$, $df = 16$) (Fig. 6). The standardized path coefficients for cropping systems are reported in Table 3. At DTC, out of 42 tested relationships, 15 were significant (Fig. 6a). The SEM revealed significant direct effects of cropping systems on soil TN, SOC, P_{avail} , soil pH, N uptake, P uptake, total colonization, litter mass loss, and grain yield (Fig. 6a; Table 3). Notably, cropping systems influenced grain yield directly with highest path coefficients observed in the CT, CT+M, NT, and NT+M systems (Fig. 6; Table 3). Cropping systems also influenced grain yield via N uptake in which the highest path coefficient was observed in the NT+M+R or via soil TN for all treatments involving mulching (i.e., CT+M, CT+M+R, NT+M, and NT+M+R) (Fig. 6; Table 3). Soil TN positively affected maize P uptake and grain yield ($\lambda = 17.8$ and 2.6 , respectively) (Fig. 6a). In turn, P uptake had direct positive effects on N uptake ($\lambda = 4.0$) and K uptake ($\lambda = 10.6$) (Fig. 6a). A significant negative effect of the AM fungal root colonization was observed on N uptake ($\lambda = -0.6$). To summarize, of the measured variables, only soil TN and N uptake had direct positive and significant effects on grain yield (Fig. 6a).

Contrary to what was observed at the sandy location, at the clay location cropping systems had no significant influence on soil TN, SOC, and pH (Fig. 6b). Soil available P had a significant positive effect on P uptake ($\lambda = 0.02$), which in turn positively affected N uptake ($\lambda = 3.9$). However, soil pH negatively affected P uptake, but positively affected TN and SOC ($\lambda = 0.82$ and $\lambda = 13.1$, respectively). Cropping systems affected grain yield directly (Table 3), and indirectly and positively via N uptake ($\lambda = 0.1$, respectively) (Fig. 6b). Cropping systems also influenced N uptake in which the highest path coefficient was observed in the NT+M+R system (Table 3). Root colonization by AM fungi showed a significant, but slightly negative relationship, with yield ($\lambda = -0.03$) (Fig. 6b).

Finally, as expected, a highly significant and positive covariance was observed between SOC and TN at both locations (Fig. 6).

4. Discussion

The application of the three components of CA in southern Africa has been variable across the region resulting in variable maize yield responses. Recently, a study by Mhlanga et al. (2021a) assessed how the different combinations of the CA components affect maize yield and stability using eight experiments ranging from two to six years. This study revealed that the application of mulch was the most crucial in enhancing yield stability as compared to the other components. However, it is important to understand how these different combinations affect soil processes that in-turn drive yield responses, and thus we present such information herein using two of the eight experiments from the study of Mhlanga et al. (2021a) having contrasting soil texture.

4.1. Soil nutrient stocks, chemical properties, and residue decomposition

In general, at both sampling times, the effects of the cropping systems on SOC, TN, P_{avail} were stronger at the sandy location as compared with the clay locations. Indeed, the soil at the clay location is generally very high in SOM as well as SOC, which was two-fold higher than at the sand location (Mhlanga et al., 2021a), thus probably masking the cropping system effect over the period of research. This has previously been confirmed by Chivenge et al. (2007) who found similar results on contrasting soils in Zimbabwe.

In agricultural systems, SOM build-up is a slow process that depends on the quantity of organic matter produced and retained in the soil (Studdert and Echeverría, 2000), as well as on the quality of the C sources that can affect microbial activity and decomposition (De Clercq et al., 2015). This means that SOC and TN in soil is generally dependent on the actual organic input, and its integration into the mineral matrix (Saint-Laurent et al., 2014). Since the region in which the study was carried out experiences long dry winters (about seven months), this means that the microbial activity and decomposition are slowed down and hence the transformation of organic inputs into SOM is reduced. Soil TN and SOC changes at the clay location were thus not detectable possibly because this location was already high in fertility. This is

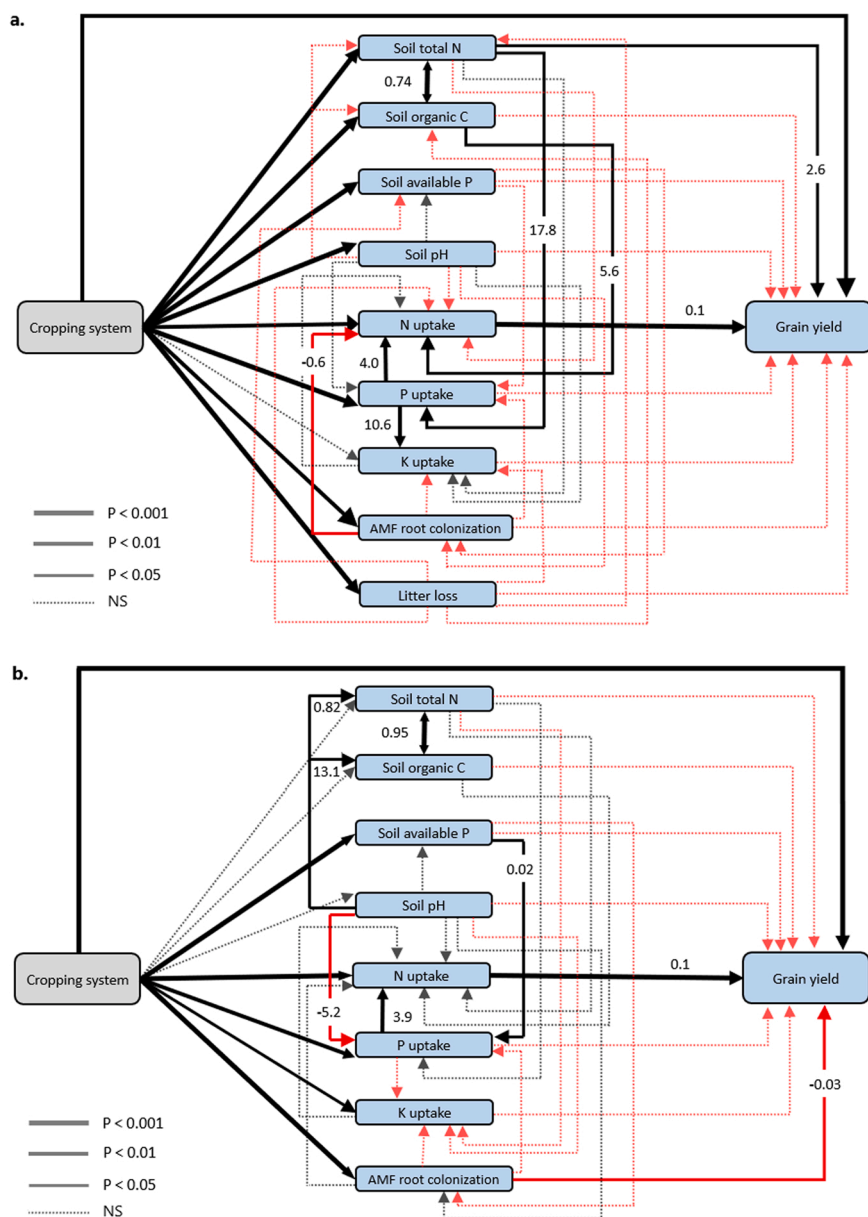


Fig. 6. Piecewise structural equation models fitted with scale standardized coefficients (λ) for Domboshava Training Center (sandy location) (Fisher's $C = 23.0$; $P = 0.29$; D.F. = 20) (a) and for University of Zimbabwe (clay location) (Fisher's $C = 15.7$; $P = 0.48$; D.F. = 16) (b). Black solid lines, denote that the drivers showed positive significant influence on the response variables while the red solid lines denote significant negative influence. The dashed lines show undetectable influence of the driver ($P > 0.05$) of which for black lines, the response was positive while for red lines was negative. The width of the arrows signifies the level of significance. For each significant path, respective standardized coefficients are presented and for the cropping system effect, the means are reported in Table 3 together with the variance explained (R^2) for each response variable. The variable full names: soil total N, soil total nitrogen; soil organic C, soil organic carbon; soil available P, soil available phosphorus; N uptake, plant nitrogen uptake; P uptake, plant phosphorus uptake; K uptake, plant potassium uptake; hyphal colonization, percentage arbuscular mycorrhizal fungal hyphal colonization of maize roots; and litter loss, decomposition of residues in litterbags.

supported by the findings of Davy and Koen (2013), Thierfelder and Wall (2012), and Mhlanga et al. (2021b) who reported under different cropping systems, non-significant changes in SOC and TN in soils having high SOM. However, in the less fertile sandy soils, the addition of mulch under no-tillage (NT+M) resulted in the highest SOC and TN, and this may be attributed to organic matter build-up over the years, promoted by crop residue retention and reduced mineralization (Ni et al., 2016). In these systems, large quantities of maize residues were retained, ensuring organic input both above- and belowground that have a high C:N ratio, meaning that the decomposition by microorganisms was slower and hence mineralization was reduced, promoting SOM build-up. Accordingly, due to the high C content, and high biomass accumulation, maize residues have been shown to add more C in the soil as compared to other cereals and legumes (Wilhelm et al., 2004; Cheesman et al., 2016).

However, other systems that include mulch, e.g., CT+M, CT+M+R, and NT+M+R, were less responsive to build up SOC and TN compared to the NT+M system and this may be attributed to the effect of plowing and rotation with a legume. In soil, fungi and bacteria are the main microbial agents of decomposition and hence practices that promote the functioning of their communities tend to promote residue

decomposition and thus lower build-up of SOC and TN. As residues decompose, microbes become strongly associated with the decomposing residues creating a substrate-microbe complex (McClougherty, 2001). Thus, conventional tillage facilitates burial of residues into soil, and this increases the contact of residues with active microbial populations (e.g., bacteria, fungi, actinomycetes) which are highly active and thrive under warm moist conditions (Vigil, 1995). This exposes the labile C pool to microbial transformation, leading to less SOC and TN build-up in conventional tillage-based systems (Fujisaki et al., 2018). On the other hand, rotating maize with cowpea and retaining its residues promote the accumulation of N and P which become available to microbes for the production of enzymes, adenosine triphosphate and other essentials of metabolism and to actively decompose even the maize residues with a wide C:N ratio (Parr and Papendick, 2015). Consequently, such systems involving rotations promote microbial activity and hence decomposition of residues.

Systems that involve mulching also promote availability of P and this is due to the release of its available forms into soil during the mineralization of OM (Ali et al., 2019). Organic molecules also compete with the P adsorbed to soil particles and thus reducing P retention in soil and

Table 3

Standardized path coefficients of cropping systems influence on different measured response variables at Domboshawa Training Center (sandy location) and at University of Zimbabwe (clay location).

Location	Cropping system	Standardized path coefficient estimates [†]									
		TN (t ha ⁻¹)	SOC (t ha ⁻¹)	P _{avail} (mg kg ⁻¹)	Soil pH	N uptake (kg ha ⁻¹)	P uptake (kg ha ⁻¹)	K uptake (kg ha ⁻¹)	AM fungal root colonization (%)	Litter loss (%)	Grain yield (t ha ⁻¹)
Domboshawa Training Center	CT	0.74c	8.23 b	30.34c	4.96 b	50.80 b	10.33 ab	142.99 a	40.33 b	73.10 b	4.44 a
	CT+M	1.03 a	11.04 a	34.51c	5.08 ab	39.90c	6.37c	122.63 a	38.42 b	78.61 ab	3.95 a
	CT+R	0.95 ab	7.96c	27.27c	5.27 a	64.91 ab	8.09 b	74.49 a	48.91 a	83.65 a	3.65 ab
	CT+M+R	1.00 a	8.58 b	80.74 a	5.28 a	64.94 ab	14.62 a	65.45 a	46.87 a	84.63 a	3.70 ab
	NT	0.77c	8.18 b	31.51c	4.90 b	56.91 b	9.26 b	107.27 a	42.07 b	78.01 ab	3.87 a
	NT+M	1.00 a	10.63 ab	76.50 b	4.95 b	46.90 b	10.06 ab	163.04 a	46.96 a	81.29 a	3.99 a
	NT+R	0.71c	6.09c	27.55c	5.14 ab	69.54 ab	12.64 ab	102.75 a	44.38 ab	75.66 b	3.44 b
	NT+M+R	0.83 b	5.91c	45.85c	5.08 ab	76.70 a	14.90 a	125.94 a	47.02 a	67.15 b	3.08 b
	P value	< 0.001	< 0.001	< 0.001	< 0.001	0.004	0.001	ns	0.006	< 0.001	0.001
	Conditional R ²	0.55	0.69	0.59	0.53	0.93	0.67	0.67	0.76	0.53	0.97
	University of Zimbabwe	CT	2.00 a	22.00 a	69.23 a	5.22 a	58.87 b	4.03 d	20.01 d	40.52 b	–
CT+M		1.94 a	21.71 a	61.69 a	5.37 a	50.67 b	11.13 a	66.96 ab	41.95 b	–	2.60c
CT+R		1.95 a	22.03 a	13.93c	5.37 a	51.66 b	12.36 a	55.91 b	44.41 ab	–	2.68c
CT+M+R		2.08 a	23.68 a	57.83 a	5.28 a	63.90 ab	8.14 abc	52.10	46.92 ab	–	3.23 a
NT		2.03 a	23.80 a	30.34 b	5.18 a	67.20 ab	4.73 d	8.19 e	44.13 ab	–	3.11 ab
NT+M		2.01 a	22.46 a	59.81 a	5.32 a	45.57c	10.13 ab	48.72c	42.29 b	–	3.22 a
NT+R		1.75 a	20.34 a	28.73 b	5.23 a	48.81c	10.81 ab	58.19 b	55.12 a	–	3.15 ab
NT+M+R		2.15 a	24.68 a	11.50c	5.28 a	77.41 a	7.67c	70.32 a	49.30 a	–	3.05 abc
P value		ns	ns	< 0.001	ns	< 0.001	< 0.001	0.002	< 0.001	–	< 0.001
Conditional R ²		0.24	0.21	0.45	0.28	0.87	0.91	0.52	0.76	–	0.92

[†] Path coefficient estimates with different letters denote groupings based on post-hoc tests. The variable full names: TN, soil total nitrogen; SOC, soil organic carbon; P_{avail}, soil available phosphorus; N uptake, plant nitrogen uptake; P uptake, plant phosphorus uptake; K uptake, plant potassium uptake; AM fungal root colonization, percentage of arbuscular mycorrhizal fungal root colonization of maize; litter loss, percentage decomposition of residues in litterbags.

increasing the availability of P. Thus, the results of the litterbag assessment in the sandy location were congruent with soil parameter responses. However, a study by [Powelson et al. \(2016\)](#) showed that a combination of three components of CA was more effective in C build-up. Based on our results, we can therefore accept the first hypothesis that CA component combinations involving mulch are more effective in improving SOM and the other soil chemical properties.

4.2. Effect of cropping systems on plant nutrient uptake and yield

The uptake of micro- and macro nutrients (e.g., N, P, K, Mg, Mn, Fe, Zn, Ca, Cu) is essential for the healthy growth and development of plants and ultimately their productivity ([White and Brown, 2010](#)). However, the uptake depends mainly on the bioavailability of the nutrients which depends mainly on their chemistry and oxidation state ([Giller and Zingore, 2021](#)). In soil environments, these minerals are mainly absorbed by plants as inorganic ions and yet most of micronutrients are present as insoluble compounds. Plants can also obtain N from amino acids or organic sources in the soil. Thus, soil and environmental properties are crucial in determining nutrient availability and cropping systems that enhance the concentration of plant accessible forms and promote their uptake by plants, are desirable.

Nutrient uptake by crop roots accounts for nearly all nutrient uptake in agroecosystems unless if foliar application is done ([Smethurst, 2004](#)). The rate of uptake depends on the nutrient concentrations in the soil solution immediately adjacent to the root and yet the nutrient concentration at the root surface depends on soil water content. Soil water content is important in promoting root growth and nutrient transport to the root surface via water flux initiated by transpiration and diffusion flux towards or away from the crop roots ([Smethurst, 2004](#)). In this regard, the consistent highest nutrient uptake observed in the NT+M+R system may be attributed to improved soil water content facilitated by the improved infiltration and the reduction in soil water loss through evaporation facilitated by mulching ([Eze et al., 2020](#)). The NT+M+R system also enhanced nutrient uptake through improving nutrient availability via mineralization of the crop residues accumulated in the system probably due to improved microbial activity ([Singh et al., 2020](#)). Similar results were also observed by [Dyck et al. \(2016\)](#) for N uptake,

when NT systems with mulch were converted to conventional tillage systems, thus this may explain our high N uptake under the CT+M+R system. Mulching and rotation preserve soil moisture and regulate soil temperature extremes, thus creating a conducive environment for microbial activity which resulted in an enhanced mineralization and thus an increased N uptake. On the other hand, the plant ability to exploit the soil profile is also an important aspect of nutrient uptake and thus the improvement of plant root traits is equally important. Conservation agriculture-based systems can improve plant root growth and development and thus the soil exploitation potential of roots ([Mondal et al., 2019](#)). The CT+M+R and NT+M+R systems also had the highest grain yield and stover, possibly due to the improved nutrient uptake and use efficiency, improved moisture and soil structure among other factors ([Ella et al., 2016](#)).

The highest P uptake was observed in the conventional tillage-based systems with either mulch or rotation, and in the NT based system with mulching. This may be attributed to higher soil microbial activity which resulted in a higher production of organic acids which solubilized more phosphate, resulting in more P being available for the uptake by crops ([Babujia et al., 2010](#)). Under conventional tillage, there is increased microporosity and aeration causing enhanced root growth and accessibility to P. On the other hand, under NT without mulching and/or rotation there may be stratification of the low mobile P hence rendering it less accessible to plants ([Logah et al., 2013](#)). Thus, our second hypothesis that the involvement of mulching in combinations with other CA components improves plant nutrient uptake can be accepted.

4.3. Effect of cropping systems on AM fungal root colonization of maize

Although other studies have investigated the effects of individual CA components on AM fungal root colonization (e.g., [Brito et al., 2012](#)), our study is the first one which investigates the effects of all possible combinations of CA components on the AM fungal root colonization of maize by native AMF. The highest AM fungal root colonization occurred under NT+R and NT+M+R systems. This was expected, because conventional tillage can potentially disrupt the mycelial network of AM fungi and affect tillage-sensitive taxa (i.e., taxa that rely on mycelia for the formation of the symbiosis), thus leading to reduced root colonization

rates. A global study has shown that reduced tillage can enhance AM fungal community diversity and result in higher colonization rates as compared with conventionally-tilled soils (Bowles et al., 2017). Moreover, crop rotations with leguminous crops, such as chickpea (*Cicer arietinum* L.), have been shown to increase AM fungal colonization of the subsequent cereal crop (Bakhshandeh et al., 2017). The legume in our study, cowpea, was previously shown to promote the AM fungal root colonization of maize either grown in rotation or intercrops with it and in general with legumes under mixed systems (Njira et al., 2017). Moreover, mulching enhances the survival of AM fungal propagules through the release of water-soluble C which stimulates AM fungal root colonization (Nyamwange et al., 2018). We, therefore, accept our third hypothesis that combining mulch with other CA components promotes the establishment of an effective symbiosis of crops with AM fungi.

4.4. Linkages between soil cropping practices, nutrient acquisition, AMF root colonization and crop productivity

Understanding the effects of cropping systems on different soil chemical, biological and agronomic aspects is important for management and decision making in farming systems. However, even more important is understanding the causal structure of cropping systems, maize production and other variables that are thought to mediate their relationships to enhance the knowledge of agroecosystem multifunctionality. To our knowledge, our study is the first to attempt to disentangle the pathways through which the components of CA or their combinations influence grain yield via soil chemical properties and plant-soil interactions. We used maize grain yield as a cropping system performance parameter because this is the main indicator used by farmers to assess the performance of a cropping system. We used RDA and SEM approaches to assess relationships and links among determinants. Our results suggest that different combinations of CA components have both direct and indirect causal influence on maize grain yield. In our study, cropping system management and N uptake directly explained the differences in grain yield. As suggested by the paths of influence, cropping systems that have more impact on N uptake will also result in more impact on yield, and this is in accordance with the results of Hammad et al. (2017) and many others before. As hypothesized, systems that involved rotations and mulching either under no-tillage or under conventional tillage i.e., NT+M+R or CT+M+R, resulted in the highest influence on crop N uptake and subsequently in the highest yield. Although earlier research has showed that most of the N that the plant uses for grain development originates from remobilization from the vegetative parts of the plant, more recent research has shown that continued post-flowering uptake from the soil is equally important (DeBruin and Butzen, 2014). This means that a season-long supply of N is important for optimal yields. Tillage may expose previously protected organic N to microorganisms, thus stimulating rapid mineralization and nitrification under aerobic conditions at the onset of the cropping season (Calderón et al., 2001). This may lead to an abrupt release of N as nitrates (NO_3^-) or ammonium (NH_4^+) in the soil hindering a season-long supply of N for crops. Thus, under NT+M+R, the degradation of organic N is gradual, and in such a buffered system, the conversion of soil TN to NO_3^- and NH_4^+ is regulated and crops will have enough N throughout the season thus leading to later season growth. This is often observed in the field when NT and CT systems are visually observed. Conventional tillage-based systems show early vigor and later tail off whereas NT systems have a slower start but later lead to greater terminal growth. Furthermore, due to poor soil structure in conventional tillage-based systems, we would expect more loss of N from the soil through denitrification and nitrate leaching, thus leading to more NO_3^- and NH_4^+ in soil during the early stages of maize growth than later in the season; (Kulagowski et al., 2021; Ruan and Philip Robertson, 2013). On top of regulating N uptake, CA systems have been shown to improve soil physical properties which lead to improved water infiltration and hence improved yield through increased moisture (Mhlanga and Thierfelder,

2021). Mulching in the CA systems also reduces soil moisture loss and moderates soil temperatures, thus improving water use efficiency. We acknowledge that the indirect cropping system effect on grain yield accounts for the effect of management practices on parameters that were not directly assessed in the SEM models, and these include weed responses, soil water availability, and rhizosphere microbial community responses. Although we measured the AM fungal root colonization of maize as a proxy for functional plant-microbe interaction, additional knowledge on the responses of rhizospheric biota communities, such as bacteria or eukaryotes (Ciccolini et al., 2016; Pellegrino et al., 2021), involved in plant growth and development would improve our mechanistic understanding.

Although many recent studies (e.g., Zhang et al., 2019; Pellegrino et al., 2015; Pellegrino et al., 2020) have shown the positive effects of AM fungi on crop yield, unexpectedly in our study AM fungi resulted in a direct but overall negative influence. However, our findings were in line with the results of Wang et al. (2018) in which AM fungi had negative effects on crop N uptake and yield, and this may be attributed to the competition for N between AM fungi and crops. Unlike in southern Africa, in highly N fertilized soils, this kind of competition was not measurable, and AM fungi did not affect yield (Polcyn et al., 2019). A molecular characterization of the AM fungal communities colonizing the roots of maize may enhance the understanding of the negative relationship observed in our study.

5. Conclusions

In this study, for the first time, using an integrated assessment based on a structural equation modeling, we dissected how the three components of CA, or their combinations influenced maize yield both directly and indirectly, through nutrient uptake, soil chemical properties, and AM fungal root colonization. Nitrogen uptake was the strongest and positive driver of production, whereas AM fungal colonization negatively affected maize production. Combining all the three components of CA resulted in the greatest influence on soil TN and N uptake. This might explain the highest yields observed under CT+M+R and NT+M+R systems. No-tillage based systems, in general, improved maize AM fungal root colonization, although this did not result in improved yields. However, we acknowledge that other important abiotic and biotic yield determining factors, such as water input and weed dynamics not measured in this study, could have been included in our analyses. Further analyses involving such factors as well as longer-term data may further improve our understanding of the drivers of yield in CA and CT cropping systems of southern Africa.

CRedit authorship contribution statement

Author Contributions: Initial idea, trial design and annual experimental set-up, C.T.; coordination of data collection in Zimbabwe and Italy, C.T., B.M., L.E., E.P.; formal data analysis, B.M.; writing original manuscript draft preparation, B.M.; 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 influenced the work reported in this paper.

Data Availability

Data used in this study is stored in a public data repository and can be made available upon reasonable request following data-sharing regulations.

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Declarations

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

Consent to participate – Not applicable., Consent for publication – Not applicable., Conflict of interest – The authors declare no competing interests whatsoever.

Code availability

The scripts used in data analyses in R environment are available from the corresponding author upon reasonable request.

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