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Crop diversification increases soil extracellular enzyme activities under no tillage: A global meta-analysis

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ABSTRACT

Conservation agriculture with three management principles has been widely adopted to alleviate the current global agricultural soils facing threats such as soil erosion and nutrient loss. However, unclear understanding of rational crop rotation and the lack of global quantitative assessment limit our deeper insight into soil nutrient cycling under conservation agriculture. Considering the important role of soil extracellular enzyme activities (EEAs) on soil nutrient cycling, a meta-analysis with 3238 observations was conducted on the effects of no tillage (NT) and legumes incorporation into rotation system (LRS) on soil EEAs. NT significantly increased the activities of C-acquiring, N-acquiring, P-acquiring, and oxidative enzymes by 18.3%, 17.4%, 7.1%, and 14.0%, respectively, while LRS significantly increased only P-acquiring enzymes. The combination of NT and legume cultivation had no significant effect on EEAs. In contrast, crop diversity had a positive effect on the NT-induced increase in EEAs. In addition, the extent of NT-induced changes varied depending on other factors. Through further analysis, we clarified the important factors affecting NT-induced changes in EEAs, such as climatic conditions, soil properties, and agronomic practices at the experimental sites. Overall, our findings provide insights into the understanding of the mechanisms of conservation agriculture impacts on the soil nutrient cycling.

1. Introduction

Soil biogeochemical cycles have an important role in agroecosystems, regulating the release and immobilize of important elements (e.g., C, N, P) in the soil (Delgado-Baquerizo et al., 2013). Soil nutrient status influences crop productivity and soil health, thus affecting the sustainability of agriculture (Sun et al., 2019). Soil microorganisms are central to the regulation of soil nutrient cycling (Wang et al., 2021). During growth, microorganisms release extracellular enzymes with different functions into the soil to decompose organic compounds for energy and nutrients (Luo et al., 2018). This process causes changes in the form and content of important elements such as C, N, and P, which affect the nutrient availability of the soil and the uptake of nutrients by the crop (Curtright and Tiemann, 2021). Thus, soil extracellular enzymes have an important role in driving soil biogeochemical nutrient cycling (Wang et al., 2021). Investigating the effects of different agricultural management practices on soil extracellular enzyme activities (EEAs) and their mechanisms is beneficial to alleviate the current global agricultural soils facing threats such as soil erosion and nutrient loss caused by unsustainable agricultural management practices, and to promote soil nutrient cycling and plant nutrient uptake, as well as to achieve sustainable agricultural development.

Conservation agriculture, with no-tillage (NT) as the core management practice, combined with rational crop rotation and permanent residue retention, has been widely studied because of its positive role in agroecosystems, especially the soil nutrient cycling (Sun et al., 2019; Xiao et al., 2021; Pittelkow et al., 2015). Due to the priming effect caused by the direct addition of exogenous organic compounds, straw

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return has been shown in several studies to promote soil nutrient cycling and increase the activity of microorganisms and extracellular enzymes (Luo et al., 2018; Liu et al., 2022a). However, NT generally affects the spatial distribution of organic compounds and microbial activity by improving the physical structure of the soil (Li et al., 2023). In contrast, different crop rotation systems affect microbial and extracellular enzyme activities by altering the quality of plant-derived organic compounds in the soil (Borase et al., 2020; Li et al., 2022a). Thus, tillage and crop rotation, which regulate the soil environment through physical disturbance and modification of plant-derived C inputs, may have less direct effects on soil EEAs than straw return measures. Their direction and extent may be influenced by a variety of factors, such as climatic conditions, soil properties, and other agronomic practices (Zuber and Villamil, 2016). Therefore, global holistic and quantitative assessments of the effects of NT and crop rotation on soil EEAs are necessary.

As one of the important principles of conservation agriculture, rational crop rotation has not been clearly defined. Characteristics such as crop productivity and soil nutrients were compared between crop rotation and monoculture in several studies (Pittelkow et al., 2015; Liu et al., 2022c; Zhao et al., 2020). In addition, replacing higher nutrient-depleting crops or fallow in the cropping system with suitable crop species is also considered a rational cropping system (Virk et al., 2021; Liu et al., 2022b). During growth, legumes have relatively low nutrient consumption and high quality plant residues by fixing N₂ from atmosphere through symbiotic associations with rhizobia, which will positively affect soil nutrient status and microbial community structure (Espinoza et al., 2020; Li et al., 2022a). Several studies have shown the positive effects of legumes cultivation on the preceding crop productivity, soil organic carbon, and microbial community structure, suggesting that legumes incorporation into rotation system (LRS) may be a rational crop rotation pattern (Zhao et al., 2022; Li et al., 2022a; Virk et al., 2021). The combination of NT and LRS may have different effects on different functions of the EEAs, which requires further study.

There is a broad diversity of soil extracellular enzyme species and functions, but those involved in the soil organic C, N, and P decomposition and oxidation are particularly crucial for soil nutrient cycling and crop nutrient uptake (Luo et al., 2018). For example, the hydrolytic C enzymes, including β-1,4-glucosidase (BG), β-1,4-xylosidase (BX), cellobiohydrolase (CBH), invertase (INV), and cellulase (CEL), are produced by microorganisms for hydrolysis of carbohydrates (Zhou et al., 2022). Key enzymes involved in microbial N acquisition, including N-acetyl-β-glucosaminidase (NAG), leucine-aminopeptidase (LAP), urease (URE), and proteases (PRO) (Luo et al., 2018). The enzymes involved in P acquisition include acid and alkaline phosphatases (AcP and AkP) (Margalef et al., 2021). As well as enzymes associated with oxidative decomposition processes, including phenol oxidase (PHO), peroxidase (PEO), dehydrogenase (DEH), and catalase (CAT) (Li et al., 2022b). The responses of these EEAs to agronomic management practices depend on the effect of management practices on soil properties, such as availability of C, N, and P resources, soil physical structure, and microbial communities (Curtright and Tiemann, 2021; Li et al., 2022b). Given that agroecosystems are influenced by multiple factors, experimental site attributes and other management practices affect the changes in soil properties induced by tillage and crop rotation, resulting in different degrees and directions of response of enzymes with different functions (Zuber and Villamil, 2016; Curtright and Tiemann, 2021). To our knowledge, despite the increasing number of field studies on the response of soil EEAs to NT and LRS, the relatively few global holistic and quantitative assessments limit our in-depth understanding of this topic (Borase et al., 2020; Chander et al., 1997; Pandey et al., 2014; Wei et al., 2014; Zhang et al., 2014; Zuber and Villamil, 2016).

We compiled a global dataset of 3238 paired observations to examine the dynamics of different functional groups of soil EEAs in response to tillage and crop rotation. We hypothesized that: (1) both NT and LRS as well as their combination would stimulate soil EEAs, (2) different functional groups of extracellular enzymes have different responses to NT and LRS, and (3) the effects of NT and LRS on EEAs will be affected by the climatic conditions, soil properties, and agronomic practices at the experimental sites.

2. Materials and methods

2.1. Data collection

We collected peer-reviewed articles published before December 2021 with the theme of "the effects of soil tillage or crop rotation on soil extracellular enzymes" through China National Knowledge Infrastructure (http://www.cnki.net) and Web of Science (http://apps. webofknowledge.com) according the following terms: "till* ", "conservation tillage", "reduc* disturbance", "rotation", "stubble", "cropping system", "legume", and "enzym* ". Among the tillage practices, notillage (NT) and conventional tillage (CT) are the treatment and control, respectively. And among the crop rotation practices, LRS represents the rotation system integrate legumes whereas those without legumes were used as the control (CK). Appropriate articles were selected based on the following criteria to obtain high-quality datasets for metaanalysis: (1) the experiments were field studies; (2) at least one soil extracellular enzyme was reported; (3) availability of information on the agronomic management practices and site of the experiments; (4) in the LRS, legumes were grown in the test plots; (5) the crop planting sequences of LRS and CK were identical except for the growing season of legumes, and no legume crops were planted in the CK group.

Based on different functions, soil extracellular enzymes were categorized as C-acquiring enzymes, N-acquiring enzymes, P-acquiring enzymes, and oxidative decomposition enzymes (Li et al., 2022b; Zhou et al., 2022). Soil C-acquiring enzymes included β -1,4-glucosidase (BG), β -1,4-xylosidase (BX), β -D-cellobiohydrolase (CBH), invertase (INV), and cellulase (CEL). Soil N-acquiring enzymes included N-acetyl- β -glucosaminidase (NAG), leucine aminopeptidase (LAP), urease (URE), and proteases (PRO). Soil P-acquiring enzymes included acid phosphatase (AcP) and alkaline phosphatase (AkP). Soil oxidative decomposition enzymes included phenol oxidase (PHO), catalase (CAT), dehydrogenase (DEH), and peroxidase (PEO). We also provided information on soil S-acquiring enzyme (arylsulfatase), though this is not discussed in depth here.

In total, 106 articles with 2500 pairwise data on soil tillage and 29 articles with 738 pairwise on crop rotation were selected. The study sites and data frequencies were presented on the world map and they were mainly distributed in China, America, Europe, India, and Brazil (Fig. 1). Detailed information on the compiled dataset is presented in the supplementary material (listed as references). Data values presented as figure were extracted using WebPlotDigitizer 4.5 (https://automeris. io/WebPlotDigitizer/). Variation was recorded and converted to standard deviation (SD). SD values were calculated from the standard error (SE) using Eq. (1):

$$SD = SE \times \sqrt{n}$$
 (1)

where n is the number of replicates. In cases where SD and SE were missing, the SD was estimated from the average coefficient of variation for the known data (Huang et al., 2018).

Because different soil extracellular enzymes within the same functional group generally performed similar functions in the soil nutrient cycle, we followed meta-analysis that grouped responses (Zhou et al., 2022): if multiple enzymes in the same functional group were reported in a field study, we used their mean values as the overall responses between treatments and controls. The corresponding SD were then calculated following the error propagation method using Eq. (2):

$$SD^2 = \sum_{i=1}^n SD_i^2 \tag{2}$$



Fig. 1. Global distribution of sites and frequencies of pairwise comparison data for meta-analysis. Dot size indicates the frequency of pairwise comparison data.

where SD_i is the SD for each soil enzyme within the same functional group. Ultimately, we use the grouped data set for subsequent meta-analysis.

Additionally, information on climate conditions [mean annual temperature (MAT), mean annual precipitation (MAP), and aridity index (AI)], soil properties [soil clay content, pH, and concentration of soil organic carbon (SOC)], and agronomic practices [cropping system, crop diversity, residue management (RM), experimental duration, and nitrogen fertilizer input (N-ferti)] was documented. When not reported, we extracted MAT, MAP, and AI from the WorldClim database (http:// www.worldclim.org/) and the Global Aridity and PET database (htt p://www.cgiarcsi.org/data/global-aridity-and-pet-database), and soil clay content, pH, SOC from the HWSD database (Regridded Harmonized World Soil Database v1.2, https://doi.org/10.3334/ORNLDAAC/1247) using geographical location information.

Specifically, in the cropping system subgroup of the tillage treatment, we divided it into legume-based cropping system, non-legumes cropping system, and monoculture. The crop species subgroup of the rotation system was defined as the type of crop that was replaced by legumes in the cropping system. The crop diversity of cropping system under different tillage practices and CK was calculated using Eq. (3):

$$Crop \quad diversity = N_{species} \times N_{group} \times N_{year} \tag{3}$$

where $N_{species}$ is the total number of crop species, N_{group} is the total number of crop functional groups, and N_{year} is the average number of crop species per year (Zhao et al., 2022).

2.2. Meta analysis

The natural log of response ratio (lnR) was chosen as the effect size (Hedges et al., 1999) and calculated using Eq. (4):

$$\ln R = \ln \left(\frac{\overline{X}_t}{\overline{X}_c}\right) = \ln \overline{X}_t - \ln \overline{X}_c \tag{4}$$

where $\overline{X_t}$ and $\overline{X_c}$ are the mean values of the soil EEAs under treatment and control, respectively. The variance (v) of each lnR was calculated using Eq. (5):

$$v = SD_t^2 / n_t \overline{X}_t^2 + SD_c^2 / n_c \overline{X}_c^2$$
(5)

where n_t and n_c are the sample sizes of the treatment and control, respectively, and SD_t and SD_c are the standard deviations of treatment and control, respectively. The overall effect size (lnR++) was calculated in the mixed-effects model by "rma.mv" function in the R package

"metafor" (Viechtbauer, 2010). Because several studies contributed more than one paired observation, and there was non-independence in the ecological meta-analysis (Noble et al., 2017). To ensure the independence of each observation, we thus considered "publication.ID" and "observation" as random factors in the mixed-effected models (Zhang et al., 2022a). To better explain the results, the percentage changes in the soil EEAs under NT and LRS than those under CT and CK were calculated using Eq. (6):

Effect size
$$(\%) = (e^{\ln R + t} - 1) \times 100\%$$
 (6)

The overall effect of NT and LRS on soil EEAs were considered if P < 0.05. Rosenthal's fail-safe number was used to determine whether there was a publication bias; when N > 5 n + 10 (where n is the number of datasets used), there was no publication bias.

To further understand how different site-experimental factors influence the lnR of soil EEAs, we evaluated the impacts of discrete variables (i.e. cropping system and residue management in tillage treatment; tillage practices and alter crop species in rotation treatment) by using the test of moderators in R package "metafor". Linear regression analysis was used to evaluate the effect of initial soil clay content, pH, SOC, MAT, MAP, AI, experiment duration, crop diversity, and N-ferti on changes in soil EEAs (lnR) in response to NT and LRS.

We used model selection analysis in the R package "glmulti" to identify essential predictors of the lnR of soil C-acquiring enzymes, Nacquiring enzymes, P-acquiring enzymes, and oxidative decomposition enzymes (Calcagno and de Mazancourt, 2010). This model selection analysis was based on maximum likelihood estimation, fitting of all possible models containing the potential predictors. The relative importance of each predictor was calculated by the sum-of- Akaike-weights for all potential models that included this predictor. This value indicated the overall support of each predictor across all possible models. A cutoff of 0.8 was chosen to differentiate between important and non-essential predictors (Terrer et al., 2016). The site-experimental factors (MAT, MAP, AI, soil clay content, pH, SOC, cropping system, crop diversity, experiment duration, residue management, and N-ferti) were incorporated into the model selection analysis. Because most of the effects of LRS on soil extracellular enzyme activities were not significant, we conducted model selection analysis on the effects of NT (Fig. 2; Table S2).



Fig. 2. Impacts of tillage and crop rotation on different soil extracellular enzyme activities. Error bars show 95% confidence intervals. The gray numbers on the left of vertical dashed lines indicate sample sizes of observations, and the "*" in the upper right corner of the number indicates the significant effect at P < 0.05.

3. Results

3.1. Overall effects

Results from this meta-analysis showed that NT significantly increased all functional groups of soil EEAs, with mean effect sizes and 95% CIs all more than zero (Fig. 2). The activities of soil C-acquiring, N-acquiring, P-acquiring, and oxidative enzymes were increased by 18.3%, 17.4%, 7.1%, and 14.0%, respectively. Specifically, BG, BX, CBH, INV, NAG, URE, PRO, AcP, AkP, CAT, DEH, and arylsulfatase showed significantly enhanced activities under NT (Table S2). However, the effect of LRS on most soil EEAs was not significant, LRS only significantly increased the P-acquiring enzyme activity.

The fail-safe numbers of soil extracellular enzymes were far greater than the number of observations (Table S3), implying that the results were virtually unaffected by publication bias (P < 0.001). Additionally, heterogeneity tests for soil extracellular enzymes were significant (P < 0.001), indicating that the observed values were not homogeneous and were influenced by other factors.

3.2. NT impacts on soil extracellular enzyme activities under different conditions

The test of moderators and linear regression analysis showed that NT-induced changes in EEAs of different functional groups were influenced by climatic conditions, soil properties, and agronomic practices (Fig. 3; Table 1). Under different climatic conditions, the lnR of N-

acquiring enzymes showed a significant negative correlation with MAT and a significant positive correlation with AI; while the lnR of oxidase had a significant positive correlation with MAP and AI. Soil properties significantly influenced the lnR of C and N-acquiring enzymes. SOC and Clay content showed significant positive and negative correlations with the lnR of C-acquiring enzymes, respectively. Whereas pH and clay content showed significant positive and negative correlations with the lnR of oxidase, respectively. The effects of different agricultural practices on the changes in soil EEAs induced by NT differed. NT-induced changes in soil EEAs in different functional groups had no significant trend under different cropping systems and the moderators test also showed non-significant results. However, crop diversity showed significant positive correlations with NT-induced changes in C and Nacquiring enzymes and oxidase activities (Fig. 3). In addition, the experimental duration showed significant positive correlations with NTinduced changes in soil EEAs in different functional groups, and nitrogen fertilizer input rate showed a significant negative correlation with lnR of N-acquiring enzymes.

When all variables were considered, the model selection analyses showed the important factors that affect NT causing changes in EEAs in different functional groups (Fig. 4). Experimental duration was consistently essential for predicting responses of soil C-, N-, and P-acquiring enzyme activities, while crop diversity was consistently essential for predicting responses of soil C, N-acquiring, and oxidative enzymes. Other important variables for predicting responses of soil C-acquiring enzymes to NT included SOC and clay content (Fig. 4a), pH for predicting responses of soil N-acquiring enzymes (Fig. 4b), as well as MAP and MAT for predicting responses of soil oxidative enzymes (Fig. 4d).

3.3. LRS impacts on soil extracellular enzyme activities under different conditions

The test of moderators showed that tillage practices only had a significant effect on the changes in P-acquiring enzymes caused by LRS, and that conventional tillage showed a higher effect than conservation tillage (Fig. S1). Different alter crop species significantly affected the changes in enzyme activities of all functional groups induced by LRS (P < 0.05), LRS-induced increase in enzyme activities was more pronounced with the replacement of fallow by legumes. The linear regression analysis showed that SOC, crop diversity, and nitrogen fertilizer input rate showed a significant negative correlation with the lnR of Cacquiring enzymes (Table S4). AI, SOC, clay content, and experimental duration showed significant negative correlations with the lnR of Nacquiring enzymes, while MAT was significant positively correlated. The lnR of P-acquiring enzymes showed significant negative correlations with AI, SOC, clay content, experimental duration, and nitrogen fertilizer input rate. In addition, MAT, MAP, AI, and nitrogen fertilizer input rate showed significant positive correlations with the lnR of oxidative enzymes, while pH was significant negatively correlated.

4. Discussion

In this study, the effects of NT and LRS on different functional groups of soil EEAs were investigated. We had hypothesized that both NT and LRS as well as their combination would stimulate soil EEAs. However, our findings were not consistent with this hypothesis. Although NT significantly increased the EEAs of different functional groups, the effect of LRS on most of the EEAs was not significant. In addition, the combination of NT and LRS (subgroup of cropping systems under NT and subgroup of tillage practices under LRS) did not significantly affect EEAs. These results suggested that rational crop rotation under conservation agriculture needs to be carefully defined. Furthermore, we found that P-acquiring enzymes respond to NT and LRS differently from other functional groups of extracellular enzymes, which was consistent with the second hypothesis. Through heterogeneity test, moderators test, linear regression, and model selection analysis, we found that the effects



Fig. 3. (a) The effects of no-tillage on different soil extracellular enzyme activities grouped by different cropping systems. Error bars show 95% confidence intervals, and the numbers above the error bars indicate sample sizes. (b) The relationships between the lnR of soil extracellular enzyme activities and crop diversity. Black lines represent the fitted linear regressions with standard error (gray shading) and dot size indicates the frequency of pairwise comparison data. L, legume-based cropping system; N, non-legume cropping system; M, monoculture; R², fitting degree; *P*, significance level; n, number of observations.

Table 1

Strength of correlations between continuous moderators and the lnR of soil extracellular enzyme activities under NT, given as slop, R² and P-value.

		MAT	MAP	AI	pH	SOC	Clay	Exp. duration	N_Ferti
C-acquiring	Slope	-0.0019	0.0001	0.0453	-0.0157	0.0051	-0.0027	0.0045	-0.0003
	R ²	-0.0004	0.0035	-0.0007	-0.0001	0.0068	0.0141	0.0102	0.0016
	Р	0.3873	0.0793	0.4563	0.3280	0.0246	0.0021	0.0075	0.1599
	n	601	601	601	601	601	601	601	601
N-acquiring	Slope	-0.0134	-0.0001	0.1753	0.0899	0.0010	-0.0061	0.0075	-0.0008
	R ²	0.0332	-0.0001	0.0061	0.0202	-0.0015	0.0103	0.0132	0.0083
	Р	< 0.001	0.3349	0.0351	< 0.001	0.7084	0.0087	0.0035	0.0167
	n	570	570	570	570	570	570	570	570
P-acquiring	Slope	0.0005	0.0001	0.0204	0.0109	-0.0013	0.0001	0.0062	0.0001
	R ²	-0.0020	0.0022	-0.0018	-0.0015	-0.0012	-0.0021	0.0112	-0.0018
	Р	0.8378	0.1506	0.6955	0.6067	0.5212	0.9324	0.0112	0.7127
	n	487	487	487	487	487	487	487	487
Oxidative	Slope	0.0001	0.0001	0.0867	0.0008	-0.0013	0.0008	0.0050	0.0003
	R ²	-0.0023	0.0291	0.0084	-0.0023	-0.0010	-0.0017	0.0088	0.0003
	Р	0.9756	< 0.001	0.0302	0.9606	0.4517	0.6012	0.0272	0.2843
	n	441	441	441	441	441	441	441	441

Bold data mean significant correlations (P < 0.05). NT, no tillage; MAT, mean annual temperature; MAP, mean annual precipitation; AI, aridity index; SOC, soil organic carbon; N_Ferti, nitrogen fertilizer input rate; Exp. duration, experiment duration.

of NT and LRS on EEAs were affected by the climatic conditions, soil properties, and agronomic practices at the experimental sites (the third hypothesis). These results suggested that the combination of conservation agriculture and rational agronomic practices under suitable climatic conditions and soil properties can positively affect agricultural sustainability by increasing soil EEAs and promoting soil nutrient cycling.

4.1. Effects of NT and LRS on soil EEAs

The present study provides robust evidence that no tillage increased the activities of soil C-acquiring, N-acquiring, P-acquiring, and oxidative enzymes, which is consistent with previous meta-analysis and field experiments (Zuber and Villamil, 2016; Chen et al., 2019; He et al., 2021). By reducing soil mechanical disturbance to farmland soils, conservation tillage improves soil aeration and moisture conditions, maintains soil T. Li et al.



Fig. 4. Model-averaged variable importance for predicting no-tillage impacts on soil (a) carbon acquiring, (b) nitrogen acquiring, (c) phosphorus acquiring, and (d) oxidative decomposition enzyme activities. Importance is based on the sum of Akaike weights derived from a model selection analysis using corrected Akaike's information criteria corrected for sample size (AICc). A cutoff of 0.8 (black dashed line) is set to differentiate between essential and nonessential variables. SOC, soil organic carbon; Exp. duration, experiment duration; N_Ferti, nitrogen fertilizer input rate; MAT, mean annual temperature; MAP, mean annual precipitation; RM, residue management.

aggregate structure, and provides suitable soil environment for microorganisms (Chen et al., 2019; Mondal and Chakraborty, 2021). In addition, higher soil C and N contents, as well as more crop residues in the soil under conservation tillage provide abundant substrate for microbial activity (He et al., 2021; Bohoussou et al., 2022). Thus, conservation tillage enhances microbial activity and stimulates the production of extracellular enzymes for energy and nutrients in their growth process, leading to the increases in soil nutrient acquisition enzyme activities (Fig. 2; Table S2; He et al., 2021; Song et al., 2022a). In addition, soils under NT have a stronger physical and chemical protection against organic matter, which reduces SOC mineralization and causes the release of soil EEAs (Kan et al., 2021; Wei et al., 2020). Notably, the increase in P-acquiring enzyme activity caused by conservation tillage was smaller than that of C-acquiring, N-acquiring, and oxidative enzyme activities (Fig. 2), which is similar to the results of He et al. (2021). Unlike C and N that can be emitted from the soil in gaseous form, the lack of an important gaseous phase of the P cycle and the sorption of P to minerals and occlusion in soils, may make the effect of NT on P availability and P-acquiring enzymes less than that of C and N elements (Cui et al., 2020; He et al., 2021; Margalef et al., 2021).

Through different quantity and quality of plant residue inputs, nutrient consumption patterns, and root activities, different cropping systems affect soil properties and microbial communities, thus altering soil EEAs (Tiemann et al., 2015; Curtright and Tiemann, 2021). Different with other crops, legumes can increase plant biomass and N content without consuming excessive soil nutrients by fixing N₂ from the atmosphere through symbiotic association with rhizobia (Espinoza et al., 2020). This process not only increases soil N availability, but also shifts the elemental stoichiometry of the soil (Li et al., 2022a). Therefore, soil EEAs may respond differently to legume cultivation. In our meta-analysis, LRS significantly increased P-acquiring enzyme activities but had no significant effect on N-acquiring enzymes (Fig. 2). The P cycle takes place mainly in the soil due to the lack of atmospheric input,

with plants and microorganisms need to mobilize and take up P from the soil, while legumes can uptake N2 from the atmosphere through symbiotic association with rhizobia (Espinoza et al., 2020; Margalef et al., 2021). Therefore, the alleviation of N limitation by increased N availability under legume cultivation stimulate microbial production of P-acquiring enzymes rather than N-acquiring enzymes (Sulieman and Tran, 2015; Hallama et al., 2021; Curtright and Tiemann, 2021). Furthermore, we found no significant effect of LRS on C-acquiring and oxidative enzyme activities, which is inconsistent with our hypothesis (Fig. 2). This may be related to the ways in which legumes are incorporated into crop rotation systems. In our dataset, the legume replaced the Gramineae accounting for a larger proportion of the field experiments and had insignificant effects on C-acquiring and oxidative enzyme activities, whereas legume substitution for fallow significantly increased soil EEAs (Fig. S1). Graminaceous produce greater biomass and input more straw and root residues into the soil than legumes (King and Blesh, 2018). The input of large amounts of active and recalcitrant organic carbon induces a stronger priming effect, prompting microorganisms to produce more C-acquiring and oxidative enzymes to obtain C and energy (Mendoza et al., 2022). Therefore, the incorporation of legume in rotation systems (such as cover crops) with increased cultivation frequency may be more conducive to the increase in soil EEAs.

4.2. Rational cropping system under NT

Several studies have shown positive effects of NT in combination with rational cropping systems on soil aggregates, organic carbon, nitrogen content, microbial communities, and crop yield (Pittelkow et al., 2015; Liu et al., 2021; Mondal and Chakraborty, 2022; Li et al., 2023). Our meta-analysis showed that crop diversity was positively associated with NT-induced increases in the EEAs, while the presence or absence of legumes in the cropping system did not have a significant effect (Fig. 3). This can be caused by the following reasons. First, soil compaction caused by NT can negatively affect crop root activities, which is detrimental to crop biomass accumulation and agricultural C input (Xiao et al., 2021). With increased crop diversity, the continued soil disturbance by root activity may have mitigated the negative effects of NT on crop growth (Lange et al., 2015). Second, crop diversification reduces the stresses to which crops are exposed under NT (e.g., weeds and diseases) by improving soil biological, biochemical and structural properties, which also has a positive impact on crop growth (Nichols et al., 2015; Zhang et al., 2022b; Zhao et al., 2022). Third, the increase in crop species under higher crop diversity allows crop residues and root exudates with different nutrient contents to enter the soil (Lange et al., 2015; Li et al., 2022a). Overall, the increased amount and diversity of C inputs promotes efficient nutrient transfer and uptake during microbial decomposition in a more suitable microenvironment under NT (Mondal and Chakraborty, 2021; Wang et al., 2022a). Ultimately, higher crop diversity under NT promotes microbial activity and therefore benefits increased EEAs. However, an increase in crop diversity, especially the temporal cultivation frequency, is often accompanied by an increase in the frequencies of N fertilizer applications, which may intensify N losses on farmland (Hamad et al., 2022). NT reduces N leaching and increasing soil available N content (Wang et al., 2020; Lv et al., 2022). Alleviation of N limitation by increased N availability may partially counteract the promotion of microbial production of N-acquiring enzymes by NT under higher crop diversity (Curtright and Tiemann, 2021). In addition, NT-induced increases in P-acquiring enzymes were more pronounced under legume cultivation compared to other cropping systems (Fig. 3). Considering the positive role of legumes in soil N and P cycling, the incorporation of legumes into cropping system may facilitate the P cycling in P-limited areas and development of rational fertilization strategies (Virk et al., 2021).

4.3. Important factors affecting the NT-induced increases in soil EEAs

Besides crop diversity, through model selection and linear regression, we identified other important factors affecting NT-induced changes in EEAs (Fig. 4). Different climatic conditions significantly affected oxidative enzyme activities under NT, with MAP and AI showing a significant positive correlation with NT-induced changes (Table 1). Generally, microbial oxidation processes are more intensive in the moister soil conditions (Toberman et al., 2008). Higher crop productivity in areas less exposed to water stress allowed more crop residues to cover the soil surface of the NT, which reduced water evaporation (Bogunovic et al., 2017; Liu et al., 2021; Li et al., 2022a). The better physical structure under NT conditions also positively affects soil moisture, which stimulates microbial production of oxidative enzymes (Toberman et al., 2008; Wardak et al., 2022). The negative correlation between clay content and NT-induced changes in C and N-acquiring enzyme activities can be explained by the larger specific surface area and better sorption capacity for labile SOC and enzymes in soils with higher clay content (Table 1; Nannipieri et al., 2018; Liu et al., 2022c). The higher clay content not only limits the physicochemical accessibility of microorganisms and their enzymes to the SOC, their adsorption and retention of enzymes also partially counteracted the increased effect of NT on C and N-acquiring enzyme activities (Table 1; Liu et al., 2021; Chen et al., 2022; Song et al., 2022b). Our study showed that SOC content was positively correlated with NT-induced increase in C-acquiring enzymes (Table 1). This is because soils with higher SOC facilitate microbial and crop growth and promote microbial production of C-acquiring enzymes (Liu et al., 2021). Unlike other functional groups of EEAs, we found a significant linear relationship between N-acquiring enzymes and different climatic conditions, soil properties, and agronomic practices under NT, which may result from the complex relationship between plant and microbial N acquisition (Table 1; Wen et al., 2021). Favorable soil moisture conditions at relatively low MAT and high AI, as well as higher pH favoring crop growth, which may intensify plant and microbial competition for available N and thus increase the production of microbial N-acquiring enzymes (Wen et al., 2021; Hao et al., 2022). In contrast, higher N fertilizer input rate increases soil N availability, alleviates N competition between plants and microorganisms as well as microbial N limitation, thus decreasing N-acquiring enzymes production and increasing biomass production and N accumulation in the residues (Chen et al., 2018). Notably, our results shown that the experimental duration is an important factor influencing the changes in EEAs under NT, which is significantly and positively correlated with all functional groups of EEAs (Table 1; Fig. 4). Previous studies have shown an improvement in soil microbial biomass carbon, SOC, and aggregate with increasing experimental duration under NT (Li et al., 2018; Liu et al., 2021). The improvement of the soil environment and microbial community by long-term NT facilitates microbial activity, thus promoting the production of extracellular enzymes by microorganisms (Li et al., 2020; Song et al., 2022a).

4.4. Limitations and implications

In this study, we defined the legumes incorporation into rotation system as a rational crop rotation in conservation agriculture and explored the effect of NT and LRS on soil EEAs. Our study showed that increased crop diversity combined with NT had a more positive effect on EEAs compared to LRS, suggesting that future studies on conservation agriculture should consider the positive effects of increased crop diversity spatially and temporally as rational cropping system on soil nutrient cycling. In general, the increases in enzyme activities indicate a positive effect of management practices on microbial activity. However, the increase of enzyme activities (such as oxidative enzymes) under some conditions may lead to a large amount of SOC decomposition and higher CO₂ emissions, which may have a negative impact on the ecological environment (Wang et al., 2022b). In addition, our results showed that NT and LRS affected the EEAs of different functional groups to a different extent, suggesting some changes in the nutrient acquisition strategies of microorganisms under conservation agriculture (Song et al., 2022a). Therefore, subsequent studies should focus on the effects of conservation agriculture on microbial strategies. The inclusion of indicators such as ecoenzyme stoichiometry and microbial carbon use efficiency in subsequent field experiments and meta-analyses will help deepen our understanding of conservation agriculture-induced changes in soil nutrient cycling and microbial communities. Meanwhile, it is worth noting that legume cultivation and increased crop diversity are non-contradictory. Given the positive effects of legumes on food security and soil ecology (Virk et al., 2021), we recommend incorporating legumes into cropping systems in a rational way to increase crop diversity (such as intercropping and cover crops). This will not only reduce crop inputs (such as fertilizers and herbicides) in agricultural production, but will also have a positive impact on soil nutrient cycling (Liu et al., 2022b).

5. Conclusion

A meta-analysis with 3238 observations was conducted on the effects of NT and LRS on soil EEAs. NT significantly increased the activities of Cacquiring, N-acquiring, P-acquiring, and oxidative enzymes, while LRS significantly increased only P-acquiring enzymes. The combination of NT and legume cultivation had no significant effect on EEAs. In contrast, crop diversity had a positive effect on the NT-induced increase in EEAs. In addition, the extent of NT-induced changes varied depending on other factors. Through further analysis, we clarified the important factors affecting NT-induced changes in EEAs, such as climatic conditions, soil properties, and agronomic practices at the experimental sites. Our findings highlight the need to further explore rational cropping systems under conservation agriculture and the response of indicators related to microbial strategies, such as ecoenzyme stoichiometry and microbial carbon use efficiency, to conservation agriculture. Overall, our findings provide insights into the understanding of the mechanisms of conservation agriculture impacts on the soil nutrient cycling.

Declaration of Competing Interest

The authors report no declarations of interest.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.still.2023.105870.

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