

Intercropping reduces soil erosion, improves soil conditions, and increases productivity of a *Camellia oleifera* plantation

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Abstract

Background and aims

Camellia oleifera, a tree species of significant ecological interest and economic value, is widely cultivated in China for its oil production. However, many *C. oleifera* plantations, particularly in the red soil regions of the Yangtze River Basin and southern China, show low productivity due to soil quality limitations. We hypothesized that intercropping would reduce soil erosion, improve soil conditions, and increase *C. oleifera* productivity.

Methods

To test this hypothesis, we intercropped *C. oleifera* with three herb species, *Parthenocissus tricuspidata*, *Coreopsis lanceolata*, and *Mentha haplocalyx*, in subtropical Hunan.

Results

Compared with monoculture, intercropping reduced runoff by 33.9–51.4%, soil loss by 72.4–84.3%, total nitrogen loss by 34.4–56.9%, and total phosphorus loss by 48.0–60.1%. Intercropping also modified soil microbial community composition, enhancing alpha diversity and promoting beneficial taxa such as Acidobacteria (31–116%) and Verrucomicrobia (15–820%). Furthermore, intercropping increased soil organic carbon by 7.4–53.8%, soil phosphorus by 2.3–56.4%, and soil urease activity by 40.4–86.0%. Most importantly, intercropping increased *C. oleifera* productivity, with the *C. oleifera* - *Parthenocissus tricuspidata* treatment yielding the highest total fruit production (134% greater than the control) and the highest total oil yield (157 kg ha⁻¹).

Conclusions

These findings support our hypothesis and demonstrate that intercropping is a sustainable land management practice for mitigating soil erosion, enhancing soil health, and boosting productivity in agroforestry systems.

1. Introduction

Camellia oleifera is a tree species of considerable horticultural importance, valued for its edible oil and ornamental appeal due to its colourful flowers. It is widely cultivated in Europe, North America, and Asia (Páscoa et al., 2018; Teixeira and Sousa, 2021; Ye et al., 2023). In China, *C. oleifera* is grown widely for oil production, with plantations reaching 4.9 million hectares spread over 15 provinces, including Hunan, Jiangxi, and Guangxi (<https://www.gov.cn/>). However, many of these plantations, especially those in the red soil regions of the Yangtze River Basin and southern China, suffer from low productivity due to soil quality limitations (Chen et al., 2023; Liu et al., 2017; Liu et al., 2018; Tan et al., 2024; Tu et al., 2019).

Red soils, which dominate subtropical China, are highly susceptible to erosion because of their poor structure, low organic matter content, and susceptibility to compaction (Gao et al., 2023; Zhang et al., 2004; Zhang et al., 2012). This vulnerability is further exacerbated by the region's hilly terrain and intense summer rainfall, characterized by short, heavy rainstorms (Li et al., 2022; Li et al., 2013; Yim et al., 2013) (<http://www.nmc.cn/>). The combination of these factors leads to severe soil runoff and nutrient loss, reducing the productivity of *C. oleifera* plantations (Chen et al., 2023; Li et al., 2019; Zhang et al., 2024). Addressing these challenges is critical to improving the sustainability and yield of cultivated *C. oleifera* in these regions.

Intercropping is the practice of growing several crop species together and is effective for reducing soil erosion by enhancing ground cover and improving soil structure (Brooker et al., 2015; Jensen et al., 2015). It is widely practiced in agricultural cropping systems and to a lesser extent in agroforestry systems. The combined canopy cover protects the soil from the direct impact of raindrops, which is a primary cause of soil particle disintegration and erosion (Liu et al., 2025). Additionally, the diverse root systems of intercropped plants, such as deep-rooted and shallow-rooted species, stabilize the soil matrix and reduce runoff. For instance, legumes with taproots and cereals with fibrous roots create a network that binds soil particles, minimizing soil erosion (Brooker et al., 2015). This synergistic effect not only preserves topsoil but also maintains soil fertility, making intercropping a sustainable solution for erosion-prone areas.

Intercropping can also enhance crop productivity by optimizing resource use and promoting environmental synergies (Liu et al., 2019 a; Ramirez-Garcia et al., 2015). The combination of crops with different growth and resource requirements allows for more efficient utilization of sunlight, water, and nutrients (Letourneau et al., 2011; Lithourgidis et al., 2011). For example, tall crops, such as maize, can provide shade for shade-tolerant species, such as beans, reducing water evaporation and improving microclimatic conditions (Kumari and Choudhary, 2022). These interactions result in higher overall yields compared with monoculture systems, demonstrating the potential of intercropping to increase agricultural productivity while maintaining ecosystem stability.

Furthermore, intercropping fosters a dynamic and resilient soil microbiome (Lu et al., 2023; Zhao et al., 2022). The presence of multiple plant species in intercropping systems leads to the exudation of diverse root secretions, such as sugars, amino acids, and organic acids, that serve as substrates for various microbial populations (Bais et al., 2006). For example, legumes in intercropping systems release flavonoids and other compounds that attract beneficial rhizobacteria and mycorrhizal fungi that play key roles in nutrient cycling and plant health (Hauggaard-Nielsen et al., 2009). In maize-bean intercropping systems, studies have shown increased abundance and activity of nitrogen-fixing bacteria, such as *Rhizobium*, and phosphate-solubilizing microbes, that enhance nutrient availability for both crops (Li et al., 2009). Moreover, intercropping promotes the coexistence of microbial taxa with complementary functions, such as decomposers, nitrogen fixers, and pathogen suppressors. In cereal-legume intercropping systems, the decomposition of legume residues provides organic matter that supports

saprophytic fungi and bacteria, while the cereal roots create a habitat for nitrifying and denitrifying bacteria (Brooker et al., 2015). This functional diversity enhances ecosystem stability and productivity.

To address soil erosion and low productivity of *C. oleifera* plantations, we introduced three plant species, *Parthenocissus tricuspidata* (PT), *Coreopsis lanceolata* (CL), and *Mentha haplocalyx* (MH), into a *C. oleifera* plantation in subtropical Hunan, China. We hypothesized that intercropping would reduce soil erosion, enhance soil nutrients and microbial activity, and increase the productivity of *C. oleifera* plantations.

The three intercropping species were chosen because their ecological and agronomic traits complement those of *C. oleifera*, making them ideal for studying the potential benefits of intercropping.

Parthenocissus tricuspidata (family Vitaceae) is a fast-growing climbing vine originating in East Asia. It has the ability to quickly cover surfaces, making it an ideal species for preventing soil erosion. Moreover, it can adapt to diverse soil conditions and tolerate shady environments (Wang et al., 2010), making it a perfect companion for *C. oleifera* plantations.

Coreopsis lanceolata (family Asteraceae) is a perennial herb native to North America (<https://plants.usda.gov/>) and widely distributed in subtropical China. *Mentha haplocalyx* (family Lamiaceae) is a common aromatic perennial herb in East Asia and is highly valued for its rich essential oil content (An et al., 2024). Both species have thick, dense foliage, which helps to retain soil moisture and improve the soil microbial activities, thus promoting the overall health of the intercropped system (Shi et al., 2018). In addition, both species are known for their ability to grow in dry and infertile soils (Folgate and Scheiner, 1992; Wang et al., 2009; Zhou et al., 2021), making them highly suitable for intercropping.

Our study had three objectives: (1) to examine how intercropping affects soil physical and chemical properties, as well as soil microbial communities; (2) to evaluate the effectiveness of different intercropping systems in reducing soil erosion and nutrient loss; and (3) to assess the impact of intercropping on *C. oleifera* fruit yield and quality. Ultimately, we aimed to determine the most effective intercropping system to minimize soil erosion and improve overall productivity for *C. oleifera* plantations in the red soil regions.

2. Material and methods

2.1 Site description

The study was conducted in a *Camellia oleifera* plantation in Shaoyang County (26°54'N, 111°22'E), Hunan Province, China. This area has a humid subtropical monsoon climate, with an average annual temperature of 18.3°C and average annual sunshine of 1610 hours (Liu et al., 2019b). The soil is mainly red soil developed from Quaternary red clay. Soil depth is usually deeper than 80 cm. Total annual rainfall is 1300 mm with the rainy season from April to June with an average rainfall of 545.4 mm. The dry

season is from July to September with an average rainfall of 273.1 mm. Soil erosion is most severe during the rainy season.

2.2 Intercropping treatment

In 2014, the intercropping treatment was conducted on a hilly site with a slope of 13–17 degrees. Leveled planting beds (approximately 1 m wide) were prepared at 3 m intervals. Three-year-old *C. oleifera* (CO) seedlings were planted in a monoculture arrangement (3 × 3 m spacing) on these beds (Fig. 1). Compound fertilizer (25% N, 10% P, and 5% K) was applied at 550–600 kg ha⁻¹ at the time of planting. Weeding was done twice (May and October). In April, 2018, twelve 15 × 20 m plots in the *C. oleifera* plantation were selected. Plots were spaced at 5 m minimum Distance. Nine of the plots were randomly intercropped with *Parthenocissus tricuspidata* (PT), *Coreopsis lanceolata* (CL), and *Mentha haplocalyx* (MH). Hereafter, these treatments are referred to as CO-PT, CO-CL, and CO-MH, respectively. The other three plots were used as controls (*C. oleifera* monoculture). For the CO-PT treatment, *P. tricuspidata* seedlings were planted at 0.5 × 0.75 m. For the CO-CL treatment, *C. lanceolata* seedlings were planted at 0.5 × 0.75 m. For the CO-MN treatment, *M. haplocalyx* seedlings were planted at 0.5 × 0.75 m.

2.3 Runoff collection system

To monitor soil erosion, a run-off collection system was set up within each plot (Fig. 1). The size of the system was 7 × 16 m. The long edge of the system was perpendicular to the contour line and the short edge was horizontal to the contour line. The system was separated from the surrounding area with an impermeable PVC hardboard buried 20 cm deep and 20 cm above ground. A drainage ditch was set up at the lower side of the system. In the system, runoff was piped and stored in the collection tanks (80 × 90 cm, diameter × height). We used a three-tank setup to account for the overflow of the system (Adimassu et al., 2020; Huo et al., 2020). The first tank was connected directly to the collection ditch with a PVC pipe. There were 10 diversion holes of 2 cm in diameter 60 cm above the bottom of the tank in the tank. One of the holes was connected to the second tank that was placed 50 cm lower than the first tank. The second tank, similar in setup to the first tank was connected to the third tank and was placed 50 cm lower than the second tank. The runoff collection was calculated as

$$Run\ off\left(m^3 \bullet ha^{-1}\right)=Tank\ 1+tank\ 2 \times 10+tank\ 3 \times 100\ (2)$$

1

The daily rainfall was recorded by a HOBO data logging rain gauge 3 (Onset Computer Corporation, USA) installed in the open area at the study site during June-August 2020. During June-August 2020, there were five rainfall events. Runoff was collected and measured immediately after each rainfall event. The runoff from all three tanks was combined and mixed thoroughly. Three 1-L subsamples were collected and returned to the laboratory for further analysis. In the laboratory, each 1-L subsample was divided into two parts. One part was used to estimate the amount of sediment in the runoff. The resultant

suspensions were filtered using Whatman 42 filter paper with a pore size of 2.5 μm. The sediment in the filter paper was oven-dried at 105°C for 24 h and weighed to obtain soil loss data. The other part was used for nutrient analysis. The total N and P concentrations were determined by potassium persulfate oxidation ultraviolet spectrophotometry and potassium persulfate oxidation molybdenum antimony resistance colorimetry (Zhang et al., 2021). Soil loss was calculated as per the equations given below:

$$Soil\ loss\left(kg\ ha^{-1}\right)=\frac{Sediment\ weight\left(g\ m^{-3}\right)\times Runoff\left(m^{-3}ha^{-1}\right)}{10^3}$$

2

Nutrient loss was calculated as per the equations given below:

$$Nutrient\ loss\left(g\ ha^{-1}\right)=\frac{Nutrent\ content\left(g\ m^{-3}\right)\times Runoff\left(m^{-3}ha^{-1}\right)}{10^3}$$

3

2.4 Fruit yield and oil content of *C. oleifera*

To compare the effects of intercropping on seed yield and quality of *C. oleifera*, we randomly selected three *C. oleifera* trees from each of the treatment plots and collected their fruits in October 2020. In total, 36 samples were collected (4 treatments × 3 replicate plots × 3 trees per plot). All fruits from each tree were harvested and weighed on-site. Three samples of about 500 g of the fruits from each plot were then brought to the laboratory for fruit trait determination. We first separated the pericarp, seed coat, and kernel and weighed them individually. They were then dried at 100–105°C for 72 h or until constant weight was reached to give dry weight. Oil content of the kernel was measured by the Soxhlet extractor method (Ye et al., 2021; Yu et al., 2023).

The following equations were used to analyze fruit quality traits (Lu et al. 2022; Ye et al. 2021):

$Total\ fruit\ yield\left(kg\bullet ha^{-1}\right)=\frac{Total\ fruit\ weight\ per\ tree\times 1156}{1000}$	(4)
$Average\ fruit\ weight=\frac{The\ weight\ of\ whole\ the\ tree\ fruit}{Fruit\ number}$	(5)
$Oil\ content\left(\%\right)=\frac{Oil\ weight}{Fruit\ weight}\times 100\%$	(6)
$Oily\ yield\left(kg\bullet ha^{-1}\right)=Total\ fruit\ yield\ per\ ha\times Oil\ content$	(7)

There were 1156 *C. oleifera* trees per hectare.

2.5 Soil physical and chemical properties and microbial diversity

Three replicate soil samples (0–30 cm) were collected from each treatment plot using a soil drill, totaling 36 samples (4 treatments × 3 plots × 3 replicate samples). The samples were placed in an ice box before transport to the laboratory. Here, each soil sample was then divided into two parts, one was used for measuring soil urease activity, polyphenol oxidase activity and soil microbial diversity. It was stored at -80°C until used. The other part of the soil sample was used for analysis of SOC, TN and total phosphorus (TP).

Soil urease activity, which measures the extracellular enzyme produced by bacteria and fungi and plant roots, was measured by phenol sodium-sodium hypochlorite colorimetric method (Domínguez et al., 2017). Soil polyphenol oxidase (PO, compounds related to polymerization of phenolic materials) was determined by pyrogallol colorimetric method (Wang et al., 2022). Soil microbial diversity (Sobs index for richness and Shannon index for diversity) was measured by the high-throughput sequencing technology (Chaudhary et al., 2021). Soil organic matter was measured by the dichromate oxidation method (Bao, 2000). total nitrogen was measured by the Kjeldahl method (Tong and Liu, 2020). Total phosphorus was measured by the ascorbic acid method (Bao, 2000). Soil pH was measured using the electrode potential method (Bao, 2000).

2.6 Statistical analyses

One-way ANOVAs and Tukey's tests were used to analyze the effect of intercropping on the yield of fruit and oil yield, soil physical and chemical properties, total water loss, total soil loss, total nitrogen and phosphorus loss, soil bacterial and fungal diversity, and abundance. Correlation analysis was used to assess the effects of fruit properties and soil physical and chemical properties, runoff, and soil erosion. Significance was accepted at $P < 0.05$. All data were analyzed by IBM SPSS statistics software (version 21.0) and Origin Pro 2016 software.

3. Results

3.1 The effects of intercropping on fruit and oil yield

Total fruit and oil yield varied significantly between the intercropping treatments and control (Table 1). The *CO-PT* treatment produced the highest total fruit yield, which was 134% higher than that of the control ($P < 0.05$). In contrast, the *CO-MH* treatment had the lowest average fruit weight (14.4 g), significantly lower than the other two intercropping treatments and the control (19.9 to 28.0 g). However, oil content was significantly higher in *CO-MH* (8.6%) than the other intercropping treatments and the control (5.8 to 6.7%). The total oil yield was highest in *CO-PT* (157 kg ha^{-1}), which was significantly higher than that of the control and the *CO-MH* treatment.

Oil content was negatively correlated with the three erosion-related indices: runoff, soil loss, and TN loss (Fig. 2). Additionally, oil content (percentage of oil in the fruit) showed a negative correlation with total fruit yield and soil total phosphorus (TP) loss, though these correlations were only marginally significant ($P = 0.07$ and $P = 0.09$, respectively).

Table 1
Effects of intercropping on fruit and oil yield of a *Camellia oleifera* plantation

Fruit and oil production	Intercropping treatment			
	Control	<i>CO-PT</i>	<i>CO-CL</i>	<i>CO-MH</i>
Total fruit yield (kg ha ⁻¹)	1093 ± 263b	2554 ± 678a	1642 ± 277ab	1003 ± 192b
Average fruit weight (g)	19.86 ± 2.63ab	26.34 ± 4.73a	27.96 ± 3.7a	14.37 ± 2.09b
Oil content (%)	5.76 ± 0.34b	6.72 ± 0.44b	6.40 ± 0.29b	8.64 ± 0.67a
Total oil yield (kg ha ⁻¹)	64.22 ± 15.74b	156.89 ± 34.64a	100.77 ± 13.95ab	84.23 ± 15.35b

All data are shown as mean ± standard error (n = 9). Different letters in the same row represent significant differences ($P < 0.05$) by Tukey's test. Intercropping treatment: Control: *C. oleifera* monoculture, *CO-PT*: *C. oleifera* + *Parthenocissus tricuspidata*, *CO-CL*: *C. oleifera* + *Coreopsis lanceolata*, *CO-MH*: *C. oleifera* + *Mentha haplocalyx*.

3.2 The effects of intercropping on soil chemical and physical properties

Intercropping strongly influenced soil chemical and physical properties (Table 2). Compared with the control, intercropping increased soil organic carbon (SOC) by 7.4 to 53.8%, TP by 2.3 to 56.4%, and soil urease activity by 40.4 to 86.0%. Intercropping also increased soil polyphenol oxidase (PO) content by 21.8% and 10.5% in *CO-CL* and *CO-MH* treatments, respectively, compared with the control, whereas no significant change was observed in the *CO-PT* treatment. In contrast, intercropping decreased soil total nitrogen (TN) by 9.5 to 33.5%. Soil pH in the control was similar to that of *CO-PT* but lower than that of *CO-CL* and *CO-MH*, but, soil bulk density showed little variation between the intercropping treatments and the control (Table 2).

Table 2
Effects of intercropping treatments on soil properties of a *Camellia oleifera* plantation

Soil properties	Intercropping treatment			
	Control	<i>CO-PT</i>	<i>CO-CL</i>	<i>CO-MH</i>
SOC (g kg ⁻¹)	8.87 ± 0.99b	9.53 ± 0.83b	13.64 ± 0.76a	13.09 ± 0.83a
TN (g kg ⁻¹)	1.58 ± 0.17a	1.31 ± 0.09ab	1.05 ± 0.1b	1.43 ± 0.13a
TP (mg kg ⁻¹)	397 ± 48b	621 ± 108a	545 ± 17ab	406 ± 62b
Urease (mg kg ⁻¹)	61.21 ± 6.74b	113.84 ± 12.43a	85.93 ± 16.65ab	100.28 ± 12.16a
PO (mg kg ⁻¹)	1007 ± 115b	958 ± 18b	1226 ± 33a	1113 ± 32ab
pH	4.43 ± 0.04bc	4.33 ± 0.09c	4.60 ± 0.04a	4.53 ± 0.03ab
Soil bulk density(g cm ⁻³)	1.41 ± 0.06a	1.46 ± 0.06a	1.46 ± 0.04a	1.45 ± 0.05a

All data are shown as mean ± standard error (n = 9). Values followed by different letters within the same row are significantly different ($P < 0.05$). Refer to Table 1 for details of intercropping treatments. SOC: soil organic carbon. TN: soil total nitrogen concentration. TP: soil total phosphorus concentration. PO: Polyphenol oxidase.

3.3 Effects of intercropping on soil erosion and nutrient losses

Across the five rainfall events, the reduction in runoff, soil loss, total nitrogen (TN) loss, and TP loss followed a consistent pattern between the intercropping treatments and the control (Fig. 3). Data from all rainfall events were combined to illustrate the total reduction in runoff and nutrient loss (Table 3). The intercropping treatments reduced total runoff by 33.9 to 51.4% compared with the control, with the reduction being statistically significant. Similarly, intercropping significantly reduced soil loss by 72.4 to 84.3%, TN loss by 34.4 to 56.9%, and TP loss by 48.0 to 60.1% compared to the control (Table 3).

Table 3
Effects of intercropping on total runoff, soil loss, and nutrient loss of a *Camellia oleifera* plantation

Soil erosion	Intercropping treatment			
	Control	<i>CO-PT</i>	<i>CO-CL</i>	<i>CO-MH</i>
Total runoff (m ³ ha ⁻¹)	38.92 ± 0.51a	25.74 ± 0.38b	21.88 ± 0.6c	18.91 ± 0.23d
Total soil loss (kg ha ⁻¹)	464 ± 18a	128 ± 5b	73 ± 4c	82 ± 3c
Total TN loss (g ha ⁻¹)	99.92 ± 2.52a	65.55 ± 1.77b	53.18 ± 2.51c	43.09 ± 1.75d
Total TP loss (g ha ⁻¹)	20.16 ± 1.16a	9.21 ± 0.63b	8.05 ± 0.57b	10.49 ± 2.03b

Values followed by different letters within the same row are significantly different

($P < 0.05$). Refer to Table 1 for details of intercropping treatment. TN: total nitrogen content in water; TP: total phosphorus content in water.

3.4 The effects of intercropping on soil microbial diversity and abundance

Soil bacterial community

Intercropping altered the relative abundance of soil bacterial communities (Fig. 4a, Table S1). The relative abundance of Chloroflexi decreased by 16.7 to 44.2% in the intercropping treatments compared with the control. In contrast, the *CO-CL* and *CO-MH* treatments increased the relative abundance of Acidobacteria by 115.9 and 95.8%, respectively, and the relative abundance of Verrucomicrobia by 820 and 481%, respectively, compared with the controls.

Diversity and richness indices (Sobs, Shannon, and Simpson) of the soil bacterial community also varied markedly between the intercropping treatments and the control (Fig. 5a). Sobs index was lowest in the control, 33.2 to 91.6% lower than that of the three intercropping treatments. Similarly, Shannon index in the control was 14.9% and 11.7% lower than that in the *CO-CL* and *CO-MH*, respectively. Simpson index was lowest in the control.

Values are percentage changes in relative abundance compared with the control. Only data showing significant changes are presented here. Refer to Table 1 for details of intercropping treatments.

Soil fungal community

Intercropping influenced the soil fungal community (Fig. 4b, Table S1). The relative abundance of Chytridiomycota decreased by 96.9 to 99.2% in the intercropping treatments compared with the control (Table S1). In contrast, relative abundance of Glomeromycota in the *CO-CL* and *CO-MH* treatments increased by 1063 and 137%, respectively (Table S1). Diversity and richness indices (Sobs, Shannon, and Simpson) of the soil fungal community varied between the intercropping treatments and the control (Fig. 5b). Sobs index was lowest in *CO-PT*, significantly lower than that of the other two intercropping treatments and the control (Table S1). Shannon index was lowest in *CO-PT*, followed by *CO-MH*, *CO-CL*, and the control. Simpson index ranged from 0.87 to 0.94 across the treatments, but the differences were not significant.

4. Discussion

4.1 Reduction in Runoff and Soil Erosion

Intercropping *Camellia oleifera* with *Parthenocissus tricuspidata*, *Coreopsis lanceolata*, and *Mentha haplocalyx* consistently reduced runoff, soil loss, and nutrient loss compared with monoculture controls. Runoff decreased by up to 51.4%, whereas soil loss was reduced by up to 84.3% (Table 3). These reductions can be attributed to the combined effects of presence of a ground cover and additional root systems, and improved soil structure. The dense foliage of the intercropped species likely served as a living mulch, reducing the kinetic energy of rain and slowing surface water flow, thereby promoting water infiltration. Additionally, the shallow root systems of the intercropped species, in contrast to the deeper roots of *C. oleifera*, probably created a network that bound soil particles, reducing their susceptibility to erosion. This mechanism aligns with findings from other agricultural systems, such as maize-bean intercropping, where complementary root architectures greatly reduced soil erosion (Li et al., 2007). Furthermore, the organic matter from leaf litter and root exudates from intercropped species enhance soil aggregation, stabilizing the soil and further mitigating erosion (Jose, 2009; Zhang et al., 2019).

Our findings align with recent studies on *C. oleifera* intercropping systems. For example, Duanyuan et al. (2023) demonstrated that intercropping *C. oleifera* with *Cassia* spp. under straw mulching reduced runoff by 28–45% and soil loss by 50–70%, corroborating our results. Similarly, Zheng et al. (2024) reported that peanut straw mulching in *C. oleifera* intercropping systems significantly reduced nitrogen loss, mirroring our observed reductions in TN (34.4–56.9%) and TP (48.0–60.1%) losses. These studies collectively highlight the effectiveness of intercropping in mitigating erosion in *C. oleifera* plantations, though the magnitude of benefits varies with companion species and management practices.

4.2 Improvement in Soil Nutrient Status

Intercropping significantly enhanced soil nutrient availability, with the most pronounced effects observed in the *CO-CL* (*Camellia oleifera*–*Coreopsis lanceolata*) and *CO-PT* (*C. oleifera*–*Pueraria thomsonii*) treatments. Soil organic carbon (SOC) was highest in *CO-CL* (13.6 g·kg⁻¹), while total phosphorus (TP) and urease activity were highest in *CO-PT*, increasing by 56.4 and 86.0%, respectively, compared with the monoculture control.

Losses of TN and TP were reduced by up to 56.9% and up to 60.1%, respectively, in the intercropping treatments (Table 3). These improvements likely resulted from three interrelated processes. First, reduced soil erosion minimizes the loss of TN and TP through runoff. Second, the diverse root systems of *C. oleifera* and the intercropped species likely accessed nutrients from different soil layers, reducing leaching and improving nutrient-use efficiency. Third, increased microbial activity enhanced the decomposition of organic matter, releasing nutrients in plant-available forms and increasing SOC, TN, and TP stocks (see more details in the microbe section below).

These findings are consistent with studies in other agroforestry systems. For example, Zhang et al. (2024) found that intercropping with legumes increased SOC by 20–40% and TP by 15–30% in Entisol soils, though their reported gains were slightly lower than ours, possibly due to differences in companion species or soil types. Notably, our results contrast with Tan et al. (2024), who observed minimal changes in TN after transforming low-yield *C. oleifera* plantations, suggesting that the choice of intercropping species (e.g., nitrogen-fixing vs. non-fixing) critically influences nutrient dynamics. Similarly, intercropping *Lycium barbarum* with grasses also increased soil TN, and urease activity (Zhu et al., 2022). Comparable benefits have been observed in coffee and cocoa agroforestry systems, where intercropping with shade trees or ground-covering plants reduced erosion and improved soil nutrient status (Isaac et al., 2012; Siles et al., 2010).

Despite the reduced losses in TN to soil erosion, soil TN was reduced by 33.5% in the *CO-CL* treatment compared with the monoculture control (Table 2). This unexpected reduction could be attributed to the greater nitrogen uptake by the intercropped species, *Coreopsis lanceolata* that may have competed with *Camellia oleifera* for available soil nitrogen, leading to faster depletion of TN. *Coreopsis lanceolata* is fast-growing and may have absorbed more nitrogen from the soil, reducing overall TN content as has been reported for other intercropping species (Jensen et al., 2015).

4.3 Enhancement of Soil Microbial Diversity

Intercropping reshaped microbial community structure, with notable shifts in the bacterial and fungal populations. Higher Sobs (richness) and Shannon (diversity) indices of soil bacteria in the intercropping treatments (Fig. 5) are indicative of improved nutrient cycling and soil health. For instance, intercropping increased the relative abundance of Acidobacteria and Verrucomicrobia by up to 116% and up to 820%, respectively (Table S1). These increases suggest enhanced nutrient cycling in intercropped systems. Both Acidobacteria and Verrucomicrobia are among the most prevalent soil bacteria in acidic environments and possess extensive carbohydrate-active enzyme systems capable of breaking down complex plant polymers like cellulose and hemicellulose (Bünger et al., 2020; Huang et al., 2023; Pinto et

al., 2020). Furthermore, the levels of Acidobacteria have been reported to positively correlate with plant growth through facilitating organic P mineralization and N cycling (Liu et al., 2024).

In the three intercropped treatments, the relative abundance of Chloroflexi decreased by up to 44.2% (Table S1). While studies have shown Chloroflexi participate in organic matter degradation and nitrogen removal (Bovio-Winkler et al., 2023), it is unclear if the reduction in Chloroflexi would have had a negative effect on soil conditions for plant growth.

The Sobs and Shannon indices of the soil fungi varied but showed no consistent patterns between the control and the three intercropping treatments (Fig. 5). The *CO-CL* treatment increased the relative abundance of Glomeromycota, a group of fungi that form symbiotic relationships with plant roots and improve nutrient uptake (Bhupenchandra et al., 2024; Zhang et al., 2020). These changes align with studies showing that diverse root exudates and organic inputs in intercropping systems create a more heterogeneous and nutrient-rich environment for microbial growth (Bais et al., 2006; Isaac et al., 2012; Van Der Heijden et al., 2008). However, the marked decrease in the relative abundance of Chytridiomycota in the intercropping treatment from 3.59–0.03% is interesting. While their role in soil nutrient cycling remains unclear, some Chytridiomycota (eg, *Synchytrium endobioticum*) are plant pathogens (Putnam and Hampson, 1989). As our analysis cannot identify fungi at the species level, the ecological implications of this reduction remain unclear.

4.4 Improvement in *Camellia oleifera* Productivity

Intercropping greatly enhanced *C. oleifera* productivity, with *CO-PT* yielding the highest total fruit production (134% greater than the control) and the highest total oil yield (157 kg ha⁻¹). Although *CO-MH* had the lowest average fruit weight, it exhibited the highest oil content (8.6%) (Table 1), showing that intercropping can improve both yield and quality. The positive correlation between oil content and soil erosion prevention (reduced runoff, soil loss, and TN loss) highlights the importance of soil conservation for *C. oleifera* productivity.

These improvements in productivity are likely driven by the synergistic interactions among the intercropped species that enhance nutrient cycling and soil fertility. In our study, these synergistic effects are evident in significant increases in SOC, TP, and urease activity, particularly in the *CO-PT* and *CO-CL* treatments. These findings align with previous studies demonstrating that intercropping systems combining deep- (the crop) and shallow-rooted plants (the herb species) create a more efficient use of soil resources, reducing interspecies competition and enhancing overall system productivity (Brooker et al., 2015; Lithourgidis et al., 2011). Similarly, intercropping increased productivity by improving soil nutrient status and microbial activity, as reported for *Lycium barbarum* with grasses (Zhu et al., 2022).

5. Conclusions

Our study demonstrates that intercropping *Camellia oleifera* with herbaceous species (*Parthenocissus tricuspidata*, *Coreopsis lanceolata*, and *Mentha haplocalyx*) significantly mitigates soil erosion, enhances

soil health, and boosts productivity in subtropical red soils. Key findings include: (1) Erosion control: Intercropping reduced runoff by 33.9–51.4% and soil loss by 72.4–84.3%, primarily through improved ground cover and root-mediated soil stabilization. These results align with global agroforestry studies but highlight the efficacy of non-legume species in erosion-prone red soils. (2) Soil health: Intercropping increased soil organic carbon (7.4–53.8%), phosphorus availability (2.3–56.4%), and urease activity (40.4–86.0%), while reshaping microbial communities toward beneficial taxa (e.g., Acidobacteria, Verrucomicrobia). Such shifts suggest enhanced nutrient cycling and resilience, critical for degraded subtropical soils. (3) Productivity gains: The *C. oleifera*–*P. tricuspidata* system achieved the highest fruit yield (134% increase) and oil production (157 kg ha⁻¹), linking soil conservation directly to economic returns. These findings highlight intercropping as a sustainable strategy for *C. oleifera* plantations in erosion-vulnerable regions.

Declarations

CRedit authorship contribution statement

Zeyao Zhao: Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. Lin Chen: Methodology, Investigation, Formal analysis. Wanwan He: Investigation, Data curation. Wenjun Xie: Investigation, Formal analysis. Byron B. Lamont: Writing – review & editing, Methodology, Conceptualization. Long sheng Chen: Investigation, Formal analysis, Methodology, Data curation. Li Mei: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. Zhaogui Yan: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources.

Declaration of competing interests

In submitting this manuscript, we provide the following statements: (1) No conflict of interest exists in the submission of this manuscript; (2) The manuscript is approved by all authors; (3) The work described was original and has not been published previously, and is not under consideration for publication elsewhere; (4) All the authors listed have made substantial contributions to the research design, or the acquisition, analysis or interpretation of data, or drafting the paper or revising it critically; and (5) Nobody who qualifies for authorship has been excluded.

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Data availability

Data will be made available on request.

References

1. Adimassu Z, Tamene L, Degefie DT (2020) The influence of grazing and cultivation on runoff, soil erosion, and soil nutrient export in the central highlands of Ethiopia. *Ecol Processes* 9(1). <https://doi.org/10.1186/s13717-020-00230-z>
2. An X, Liao Y, Yu Y, Fan J, Wan J, Wei Y, Ouyang Z (2024) Effects of MhMYB1 and MhMYB2 transcription factors on the monoterpenoid biosynthesis pathway in l-menthol chemotype of *Mentha haplocalyx* Briq. *Planta* 260(1). <https://doi.org/10.1007/s00425-024-04441-y>
3. Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu Rev Plant Biol* 57(1):233–266. <https://doi.org/10.1146/annurev.arplant.57.032905.105159>
4. Bao S (2000) *Tu rang nong hua fen xi* [Soil agrochemical analysis]. China Agriculture
5. Bhupenchandra I, Chongtham SK, Devi AG, Dutta P, Sahoo MR, Mohanty S, Swapnil P (2024) Unlocking the potential of Arbuscular Mycorrhizal Fungi: exploring role in plant growth promotion, nutrient uptake mechanisms, biotic stress alleviation, and sustaining agricultural production systems. *J Plant Growth Regul*. <https://doi.org/10.1007/s00344-024-11467-9>
6. Bovio-Winkler P, Guerrero LD, Erijman L, Oyarzúa P, Suárez-Ojeda ME, Cabezas A, Etchebehere C (2023) Genome-centric metagenomic insights into the role of Chloroflexi in anammox, activated sludge and methanogenic reactors. *BMC microbiol*, 23(1). <https://doi.org/ARTN4510.1186/s12866-023-02765-5>
7. Brooker RW, Bennett AE, Cong WF, Daniell TJ, George TS, Hallett PD, White PJ (2015) Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. *New Phytol* 206(1):107–117. <https://doi.org/10.1111/nph.13132>
8. Bünger W, Jiang X, Müller J, Hurek T, Reinhold-Hurek B (2020) Novel cultivated endophytic Verrucomicrobia reveal deep-rooting traits of bacteria to associate with plants. *Sci Rep* 10(1). <https://doi.org/10.1038/s41598-020-65277-6>
9. Chaudhary P, Sharma A, Chaudhary A, Khati P, Gangola S, Maithani D (2021) Illumina based high throughput analysis of microbial diversity of maize rhizosphere treated with nanocompounds and *Bacillus* sp. *Appl Soil Ecol* 159. <https://doi.org/10.1016/j.apsoil.2020.103836>
10. Chen Y, Zheng J, Yang Z, Xu C, Liao P, Pu S, El-Kassaby Y, Feng J (2023) Role of soil nutrient elements transport on *Camellia oleifera* yield under different soil types. *BMC Plant Biol* 23(1). <https://doi.org/10.1186/s12870-023-04352-2>
11. Domínguez MT, Holthof E, Smith AR, Koller E, Emmett BA (2017) Contrasting response of summer soil respiration and enzyme activities to long-term warming and drought in a wet shrubland (NE Wales, UK). *Appl Soil Ecol* 110:151–155. <https://doi.org/10.1016/j.apsoil.2016.11.003>
12. Duanyuan H, Zhou T, He Z, Peng Y, Lei J, Dong J, Wu X, Wang J, Yan W (2023) Effects of straw mulching on soil properties and enzyme activities of *Camellia oleifera*-*Cassia* intercropping agroforestry systems. *Plants (Basel)* 12(17). <https://doi.org/10.3390/plants12173046>

13. Folgate LA, Scheiner SM (1992) Distribution of a restricted locally abundant species: effects of competition and nutrients on *Coreopsis Lanceolata*. *Am Midl Nat* 128(2):254–269.
<https://doi.org/10.2307/2426459>
14. Gao J, Shi C, Yang J, Yue H, Liu Y, Chen B (2023) Analysis of spatiotemporal heterogeneity and influencing factors of soil erosion in a typical erosion zone of the southern red soil region, China. *Ecol Ind* 154. <https://doi.org/10.1016/j.ecolind.2023.110590>
15. Hauggaard-Nielsen H, Gooding M, Ambus P, Corre-Hellou G, Crozat Y, Dahlmann C, Jensen ES (2009) Pea–barley intercropping for efficient symbiotic N₂-fixation, soil N acquisition and use of other nutrients in European organic cropping systems. *Field Crops Res* 113(1):64–71.
<https://doi.org/10.1016/j.fcr.2009.04.009>
16. Huang J, Gao K, Yang L, Lu Y (2023) Successional action of Bacteroidota and Firmicutes in decomposing straw polymers in a paddy soil. *Environ Microbiome* 18(1).
<https://doi.org/10.1186/s40793-023-00533-6>
17. Huo J, Liu C, Yu X, Chen L, Zheng W, Yang Y, Yin C (2020) Direct and indirect effects of rainfall and vegetation coverage on runoff, soil loss, and nutrient loss in a semi-humid climate. *Hydrol Process* 35(1). <https://doi.org/10.1002/hyp.13985>
18. <https://plants.usda.gov/> (accessed 10 April 2025)
19. https:// (accessed 10 April 2025)
20. http:// (accessed 10 April 2025)
21. Isaac ME, Hinsinger P, Harmand JM (2012) Nitrogen and phosphorus economy of a legume tree-cereal intercropping system under controlled conditions. *Sci Total Environ* 434:71–78.
<https://doi.org/10.1016/j.scitotenv.2011.12.071>
22. Jensen ES, Bedoussac L, Carlsson G, Journet E-P, Justes E, Hauggaard-Nielsen H (2015) Enhancing yields in organic crop production by eco-functional intensification. *Sustainable Agric Res* 4(3).
<https://doi.org/10.5539/sar.v4n3p42>
23. Jose S (2009) Agroforestry for ecosystem services and environmental benefits: an overview. *Agroforest Syst* 76(1):1–10. <https://doi.org/10.1007/s10457-009-9229-7>
24. Kumari A, Choudhary M (2022) Annual intercrops: an alternative pathway for sustainable horticultural production. *Ecol Environ Conserv* 28(08):S244–S251.
<https://doi.org/10.53550/EEC.2022.v28i08s.037>
25. Letourneau DK, Armbrrecht I, Rivera BS, Lerma JM, Carmona EJ, Daza MC, Trujillo AR (2011) Does plant diversity benefit agroecosystems? A synthetic review. *Ecol Appl* 21(1):9–21.
<https://doi.org/10.1890/09-2026.1>
26. Li J, Wu Z, Yuan J (2019) Impact of agro-farming activities on microbial diversity of acidic red soils in a *Camellia Oleifera* Forest. *Revista Brasileira de Ciência do Solo*, p 43.
<https://doi.org/10.1590/18069657rbcs20190044>
27. Li L, Li S, Sun J, Zhou L, Bao X, Zhang H, Zhang F (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Agricultural Sci*

- 104(27):11192–11196. <https://doi.org/10.1073/pnas.070459110>
28. Li L, Zhu W, Liu J, Zhang L, Zhu L, Wang L, Gurung SB (2022) Study on multidimensional changes of rainfall erosivity during 1970–2017 in the North–South Transition Zone, China. *Front Environ Sci* 10. <https://doi.org/10.3389/fenvs.2022.969522>
29. Li Y-Y, Yu C-B, Cheng X, Li C-J, Sun J-H, Zhang F-S, Li L (2009) Intercropping alleviates the inhibitory effect of N fertilization on nodulation and symbiotic N₂ fixation of faba bean. *Plant Soil* 323(1–2):295–308. <https://doi.org/10.1007/s11104-009-9938-8>
30. Li Z, Huang J, Zeng G, Nie X, Ma W, Yu W, Zhang J (2013) Effect of erosion on productivity in subtropical red soil hilly region: A Multi-Scale Spatio-temporal study by simulated rainfall. *PLoS ONE* 8(10). <https://doi.org/10.1371/journal.pone.0077838>
31. Lithourgidis AS, Dordas CA, Damalas CA, Vlachostergios DN (2011) Annual intercrops: an alternative pathway for sustainable agriculture. *Aust J Crop Sci* 5(4):396–410. <https://www.researchgate.net/publication/224934832>
32. Liu C, Jin Y, Hu Y, Tang J, Xiong Q, Xu M, Beng KC (2019) a Drivers of soil bacterial community structure and diversity in tropical agroforestry systems. *Agriculture, Ecosystems & Environment*, 278: 24–34. <https://doi.org/10.1016/j.agee.2019.03.015>
33. Liu H, Gao X, Li C, Cai Y, Song X, Zhao X (2025) Intercropping increases plant water availability and water use efficiency: A synthesis. *Agric Ecosyst Environ* 379. <https://doi.org/10.1016/j.agee.2024.109360>
34. Liu J, Wu L, Chen D, Li M, Wei C (2017) Soil quality assessment of different *Camellia oleifera* stands in mid-subtropical China. *Appl Soil Ecol* 113:29–35. <https://doi.org/10.1016/j.apsoil.2017.01.010>
35. Liu J, Wu L, Chen D, Yu Z, Wei C (2018) Development of a soil quality index for *Camellia oleifera* forestland yield under three different parent materials in Southern China. *Soil Tillage Res* 176:45–50. <https://doi.org/10.1016/j.still.2017.09.013>
36. Liu Q, Cui H, Yang W, Wang F, Liao H, Zhu Q, Lu P (2024) Soil conditioner improves soil properties, regulates microbial communities, and increases yield and quality of *Uncaria rhynchophylla*. *Sci Rep* 14(1). <https://doi.org/10.1038/s41598-024-64362-4>
37. Liu Z, Zhang J, Zhang Y, Lao J, Liu Y, Wang H, Jiang B 2019 b. Effects and interaction of meteorological factors on influenza: Based on the surveillance data in Shaoyang, China. *Environ Res*, 172: 326–332. <https://doi.org/10.1016/j.envres.2019.01.053>
38. Lu P, Zhao C, Yin W, Hu F, Fan Z, Yu A, Fan H (2023) Microbial Community Shifts with soil properties and enzyme activities in Inter-/Mono-Cropping systems in response to tillage. *Agronomy* 13(11). <https://doi.org/10.3390/agronomy13112707>
39. Lu Y, Si Y, Zhang L, Sun Y, Su S (2022) Effects of canopy position and microclimate on fruit development and quality of *Camellia oleifera*. *Agronomy* 12(9). <https://doi.org/10.3390/agronomy12092158>
40. Páscoa RNMJ, Teixeira AM, Sousa C (2018) Antioxidant capacity of *Camellia japonica* cultivars assessed by near- and mid-infrared spectroscopy. *Planta* 249(4):1053–1062.

<https://doi.org/10.1007/s00425-018-3062-z>

41. Pinto OHB, Costa FS, Rodrigues GR, da Costa RA, da Rocha Fernandes G, Júnior ORP, Barreto CC (2020) Soil acidobacteria strain AB23 resistance to Oxidative stress through production of Carotenoids. *Microb Ecol* 81(1):169–179. <https://doi.org/10.1007/s00248-020-01548-z>
42. Putnam ML, Hampson M (1989) Rediscovery of synchytrium endobioticum in Maryland. *Am Potato J* 66:495–501. <https://doi.org/10.1007/BF02855441>
43. Ramirez-Garcia J, Martens HJ, Quemada M, Thorup-Kristensen K (2015) Intercropping effect on root growth and nitrogen uptake at different nitrogen levels. *J Plant Ecol* 8(4):380–389. <https://doi.org/10.1093/jpe/rtu024>
44. Shi S, Tian L, Ma L, Tian C (2018) Community structure of rhizomicrobiomes in four medicinal herbs and its implication on growth management. *Microbiology* 87(3):425–436. <https://doi.org/10.1134/S0026261718030098>
45. Siles P, Harmand JM, Vaast P (2010) Effects of inga densiflora on the microclimate of coffee (*Coffea arabica* L.) and overall biomass under optimal growing conditions in Costa Rica. *Agroforest Syst* 78(3):269–286. <https://doi.org/10.1007/s10457-009-9241-y>
46. Tan Z, Liu T, Ning C, Lin X, Liu X, Jiang M, Yan W (2024) Effects of transformation of inefficient *Camellia oleifera* plantation on soil quality and fungal communities. *Forests* 15(4). <https://doi.org/10.3390/f15040603>
47. Teixeira AM, Sousa C (2021) A review on the biological activity of *Camellia* species. *Molecules* 26(8). <https://doi.org/10.3390/molecules26082178>
48. Tong Y, Liu B (2020) Test research of different material made garbage enzyme's effect to soil total nitrogen and organic matter. *IOP Conference Series: Earth and Environmental Science*, 510(4). <https://doi.org/10.1088/1755-1315/510/4/042015>
49. Tu J, Chen J, Zhou J, Ai W, Chen L (2019) Plantation quality assessment of *Camellia oleifera* in mid-subtropical China. *Soil Tillage Res* 186:249–258. <https://doi.org/10.1016/j.still.2018.10.023>
50. n Der Heijden MGA, Bardgett RD, Van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol Lett* 11(3):296–310. <https://doi.org/10.1111/j.1461-0248.2007.01139.x>
51. Wang Z, Wu L, Liu T (2009) Revegetation of steep rocky slopes: Planting climbing vegetation species in artificially drilled holes. *Ecol Eng* 35(7):1079–1084. <https://doi.org/10.1016/j.ecoleng.2009.03.021>
52. Wang Z, Wu L, ANIMESH S (2010) Growth and nutrient status in climbing plant (*Parthenocissus tricuspidata* (Siebold & Zucc.) Planch.) seedling in response to soil water availability. *Bot Stud* 51:155–162
53. Wang Z, Zhou M, Liu H, Huang C, Ma Y, Ge H, Fu S (2022) Pecan agroforestry systems improve soil quality by stimulating enzyme activity. *PeerJ* 10. <https://doi.org/10.7717/peerj.12663>
54. Ye C, He Z, Peng J, Wang R, Wang X, Fu M, Tian B (2023) Genomic and genetic advances of oiltea-camellia (*Camellia oleifera*). *Front Plant Sci* 14. <https://doi.org/10.3389/fpls.2023.1101766>

55. Ye H, Chen Z, Jia T, Su Q, Su S (2021) Response of different organic mulch treatments on yield and quality of *Camellia oleifera*. *Agric Water Manage* 245. <https://doi.org/10.1016/j.agwat.2020.106654>
56. Yim S, Wang B, Xing W (2013) Prediction of early summer rainfall over south China by a physical-empirical model. *Clim Dyn* 43(7–8):1883–1891. <https://doi.org/10.1007/s00382-013-2014-3>
57. Yu X, Song Q, Liu Y, Zhang Y, Ji K, Chen L, Yuan D (2023) Effects of post-harvest natural drying on seed quality and endogenous hormones of *Camellia oleifera*. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 51(1). <https://doi.org/10.15835/nbha51113051>
58. Zhang M, He Z, Wilson MJ (2004) Chemical and physical characteristics of red soils from Zhejiang province, southern China. *Red soil China* 63–87. https://doi.org/10.1007/978-1-4020-2138-1_5
59. Zhang R, Mu Y, Li X, Li S, Sang P, Wang X, Xu N (2020) Response of the arbuscular mycorrhizal fungi diversity and community in maize and soybean rhizosphere soil and roots to intercropping systems with different nitrogen application rates. *Sci Total Environ* 740. <https://doi.org/10.1016/j.scitotenv.2020.139810>
60. Zhang X, Gao G, Wu Z, Wen X, Zhong H, Zhong Z, Gai X (2019) Agroforestry alters the rhizosphere soil bacterial and fungal communities of moso bamboo plantations in subtropical China. *Appl Soil Ecol* 143:192–200. <https://doi.org/10.1016/j.apsoil.2019.07.019>
61. Zhang X, Li Z, Zeng G, Xia X, Yang L, Wu J (2012) Erosion effects on soil properties of the unique red soil hilly region of the economic development zone in southern China. *Environ Earth Sci* 67(6):1725–1734. <https://doi.org/10.1007/s12665-012-1616-0>
62. Zhang Y, Lei J, Peng Y, Chen X, Li B, Chen Y, Yan W (2024) Impact of intercropping on nitrogen and phosphorus nutrient loss in *Camellia oleifera* Forests on Entisol Soil. *Forests* 15(3). <https://doi.org/10.3390/f15030461>
63. Zhang Y, Yan J, Rong X, Han Y, Yang Z, Hou K, Hu W (2021) Responses of maize yield, nitrogen and phosphorus runoff losses and soil properties to biochar and organic fertilizer application in a light-loamy fluvo-aquic soil. *Agriculture, Ecosystems & Environment*, p 314. <https://doi.org/10.1016/j.agee.2021.107433>
64. Zhao X, Dong Q, Han Y, Zhang K, Shi X, Yang X, Yu H (2022) Maize/peanut intercropping improves nutrient uptake of side-row maize and system microbial community diversity. *BMC Microbiol* 22(1). <https://doi.org/10.1186/s12866-021-02425-6>
65. Zheng W, Hu L, Peng Y, Wu J, Yan W (2024) Effect of peanut straw mulching on the soil nitrogen change and functional genes in the *Camellia oleifera* intercropping system. *J Soils Sediments* 24(10):3473–3484. <https://doi.org/10.1007/s11368-024-03896-6>
66. Zhou M, Wei Y, Wang J, Liang M, Zhao G (2021) Salinity-Induced alterations in physiological and biochemical processes of Blessed Thistle and Peppermint. *J Soil Sci Plant Nutr* 21(4):2857–2870. <https://doi.org/10.1007/s42729-021-00572-3>
67. Zhu L, He J, Tian Y, Li X, Li Y, Wang F, Qin K, Wang J (2022) Intercropping Wolfberry with Gramineae plants improves productivity and soil quality. *Sci Hort* 292. <https://doi.org/10.1016/j.scienta.2021.110632>

Figures

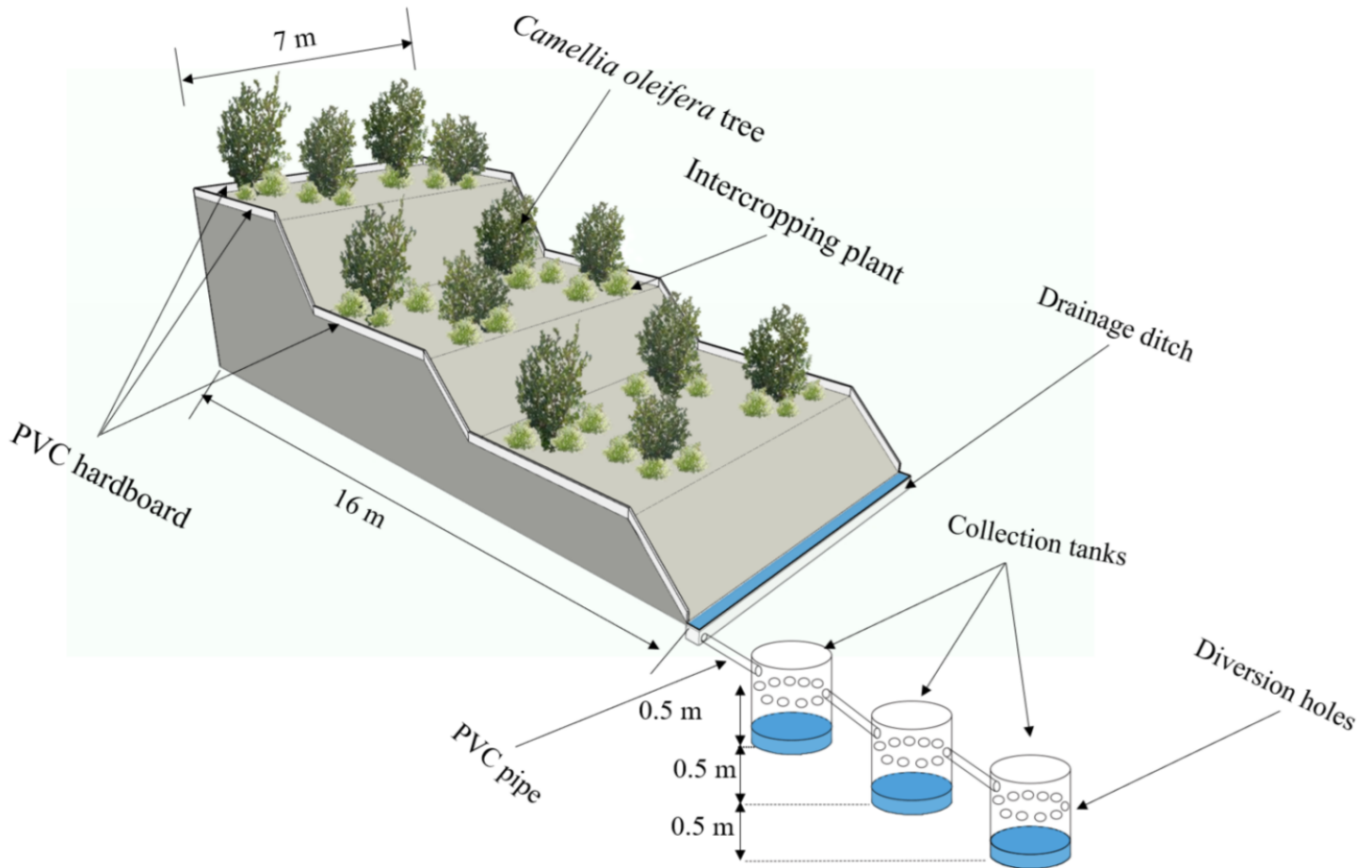


Figure 1

Runoff collection system. The plot was delineated by PVC hardboard on three sides. On the fourth side (the lower side), a metal drainage ditch was constructed for runoff collection. Runoff from the ditch was piped to a three-tank system. Ten 2 cm diameter diversion holes were drilled in the first and second tanks, with the 10th hole used for connecting the first and second tanks and the second and third tanks via PVC piping.

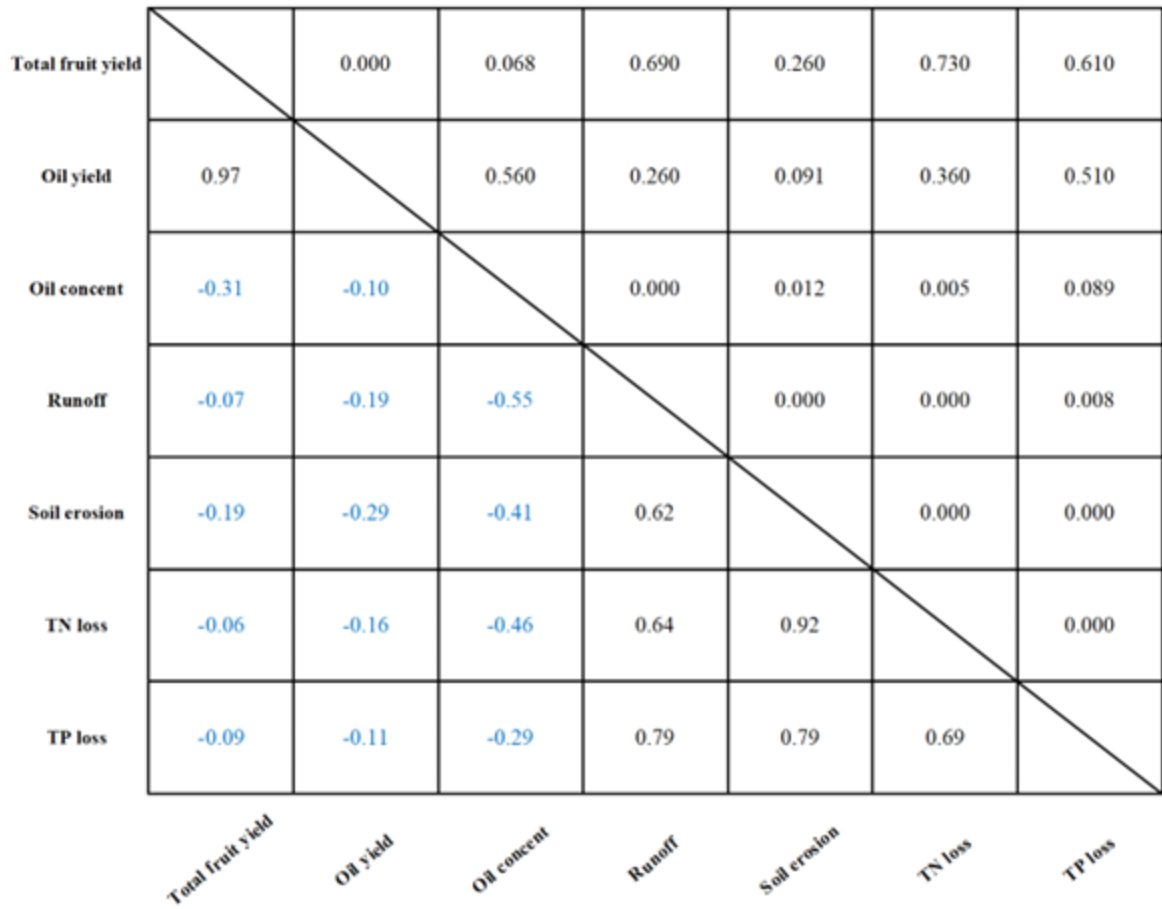


Figure 2

Correlation analysis of soil erosion and fruit production of a *Camellia oleifera* plantation. Lower triangular matrix designates correlation coefficients (Black and blue numbers designate positive and negative correlation coefficients respectively). Upper triangular matrix designates *P* value. TN: total nitrogen content in water. TP: total phosphorus content in water.

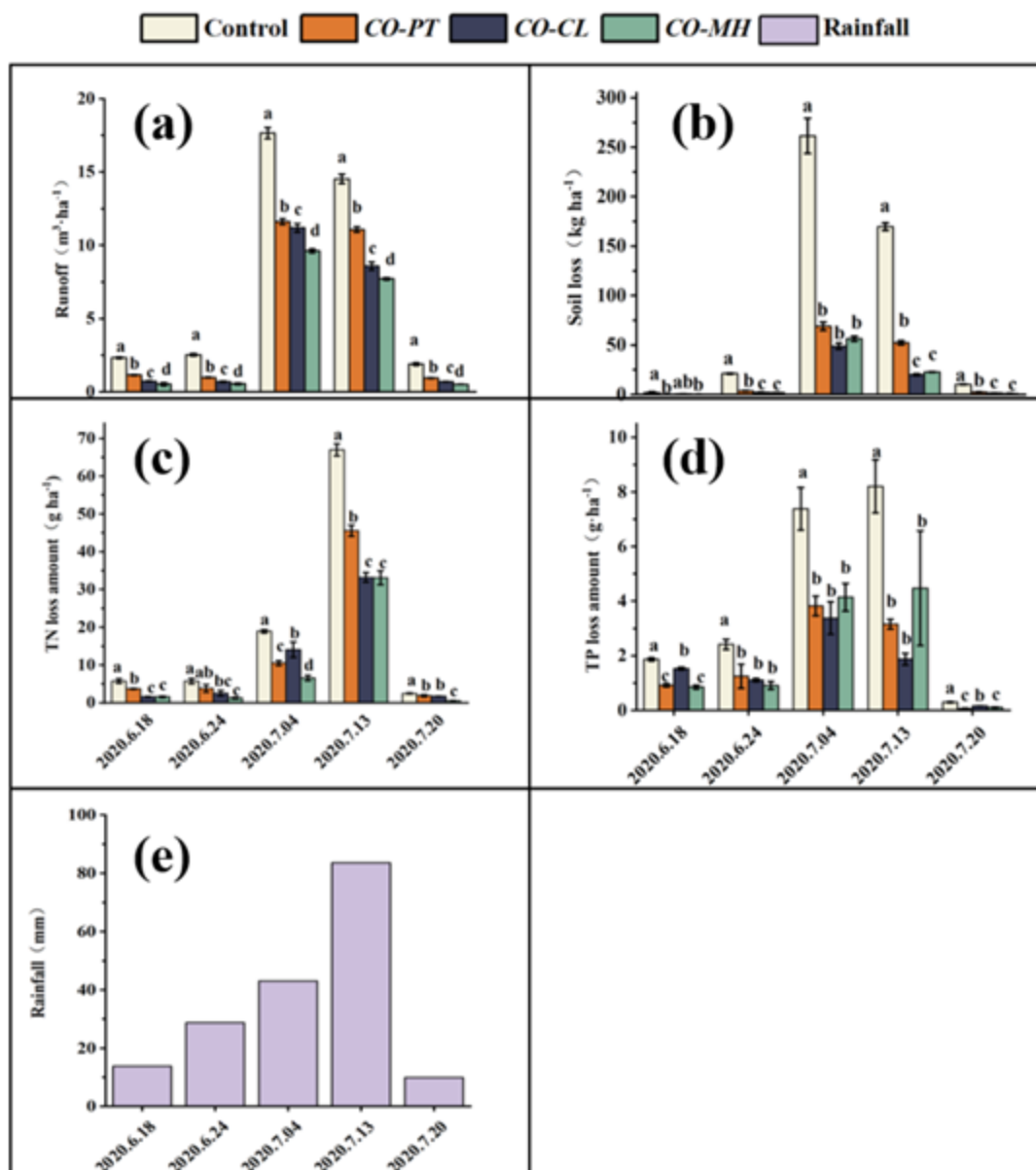


Figure 3

The effects of intercropping on runoff, soil loss, and nutrient loss in a *Camellia oleifera* plantation. TN: total nitrogen content in water. TP: total phosphorus content in water. (a) runoff; (b) soil loss; (c) TN loss; (d) TP loss; (e) Rainfall. Numbers above columns are the levels of significance according to Tukey's test (at $P < 0.05$). Refer to Table 1 for details of intercropping treatments.

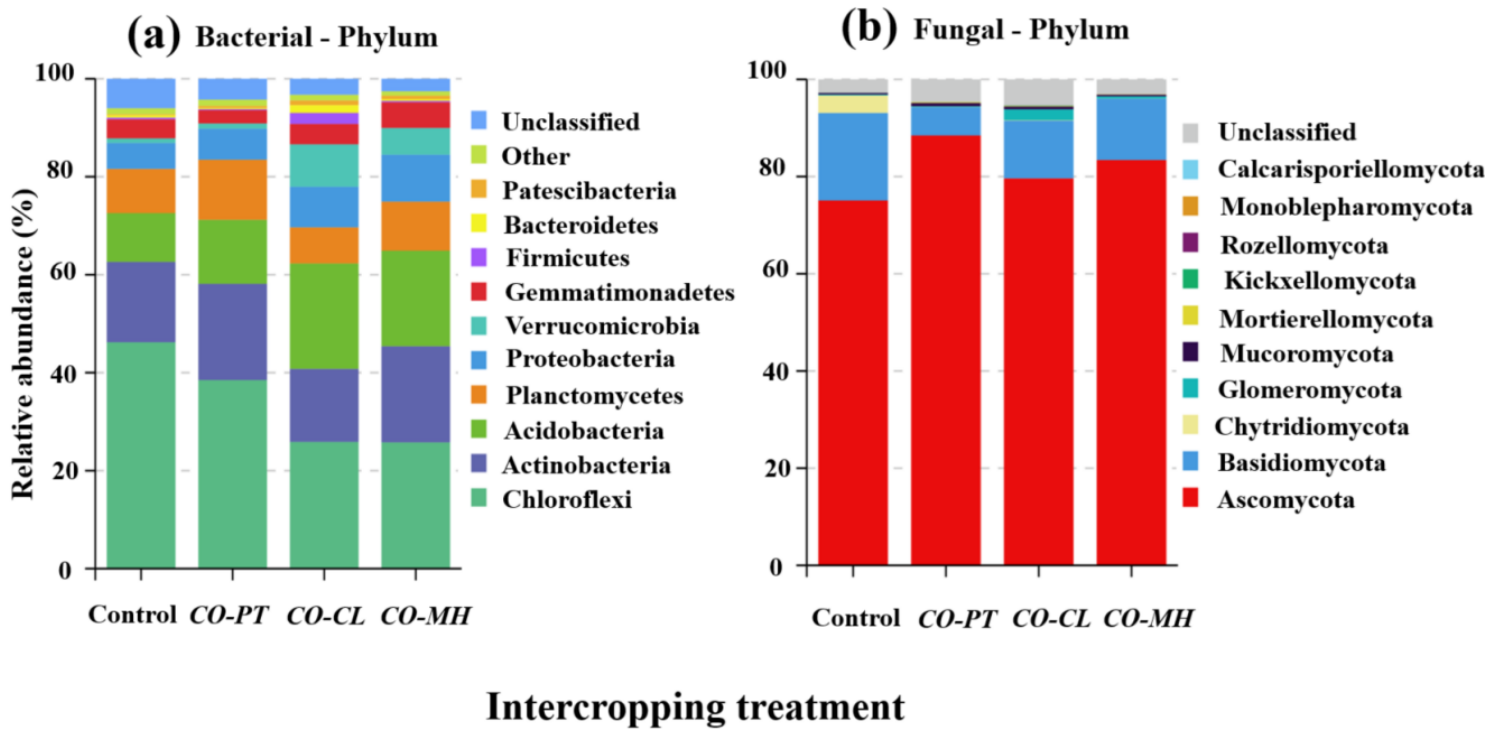


Figure 4

Composition and relative abundance of top 10 soil microflora in a *Camellia oleifera* plantation under three intercropping treatments and control. (a) phylum level of soil bacterial communities; (b) phylum level of soil fungal communities. Refer to Table 1 for details of intercropping treatments.

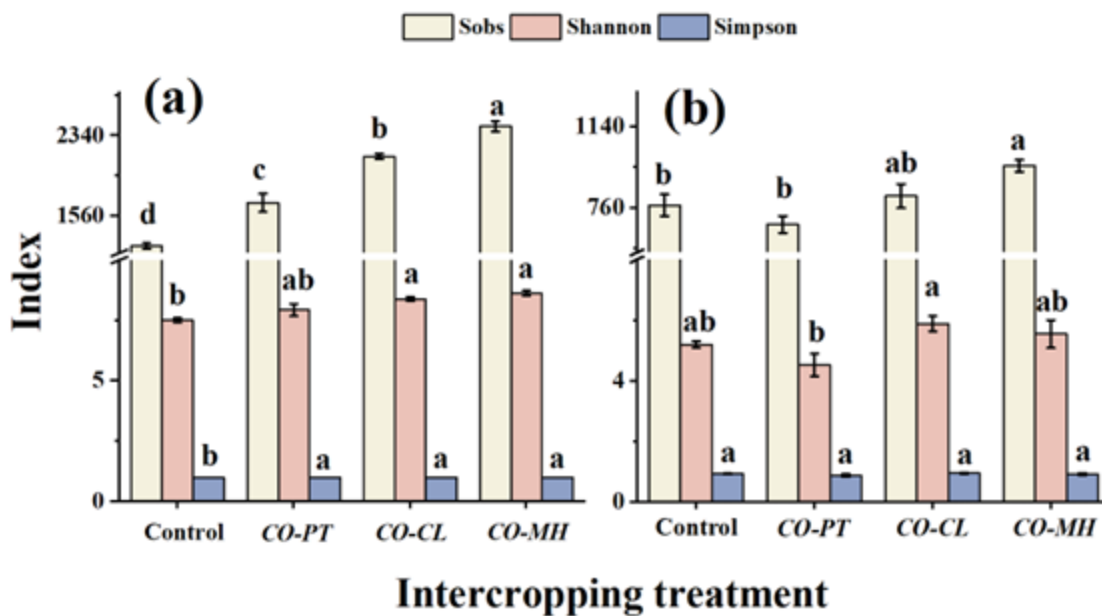


Figure 5

Alpha diversity (Sobs, Shannon, and Simpson indices) of soil bacterial community (a) and fungal community (b) in a *Camellia oleifera* plantation subject to intercropping treatments. Different letters above bars designate significant difference between intercropping treatments ($P < 0.05$). Refer to Table 1 for details of intercropping treatments.