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Progress and perspective on intercropping patterns in tea plantations

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Abstract

Intercropping, as one of the complex ecological cultivations, is an important tea plantation pattern. Compared to sole-cropping tea plantations, intercropping can improve the above- and below-ground environment, which is beneficial to tea plant growth, the formation of high tea quality and the increase of tea yield. In this review, we summarized the impacts of intercropping on the tea plantation environment (microclimate, biomass, soil nutrients, microorganisms and heavy metals), tea plants growth and tea yield. We then analyzed how intercropping affects the growth and metabolism of tea plants based on the impact of intercropping on the environment. As a result, the achievements and progress of tea plantation intercropping are summarized, the remaining problems of the current research on intercropping tea plantations are highlighted, and provide new insights for the advanced research of intercropping in tea plantations.

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Introduction

Tea is a brewed beverage made from fresh tea leaves using different processing methods and is of great interest and consumed by people worldwide. Tea plant [*Camellia sinensis* (L.) O. Kuntze] is a perennial cash crop that is suitable for growing in tropical and subtropical regions over 50 countries in the world[1]. In China, monoculture is the main planting pattern of tea plantations. However, along with advantages reported from the intercropping pattern, the acres of intercropping tea plantations are constantly expanding. Intercropping is a recommended planting pattern that is essential for low-input or resource-limited agricultural patterns[2]. This pattern is that one (or more) herbaceous/shrubby crops and trees are simultaneously cultivated on the same field, and it exploits plant growth characteristics and functional diversity to improve resource utilization and benefit all crops[2,3].

Intercropping is an efficient planting pattern widely used in agriculture. Most intercropping patterns can improve microclimate, pests and soil physical properties, which would improve crop yield and quality[4,5]. Intercropping could change the above- and below-ground environment in which crops grow, so they can affect crop growth and development[6]. In general, intercropping could significantly improve the environment such as temperature, water and light that are needed for plant growth and reduce the risk of abiotic stress on all crops[2]. Beans (*Phaseolus vulgaris*), squash (*Cucurbita* spp.) and maize (*Zea mays* L.) intercropping is a representative example that makes full use of ecological resources. In summer, squash can cover the ground, which reduces weeds and evaporation. Then, beans and maize are able to keep canopy moisture and improve light utilization during growth[7]. Additionally, intercropping also improves soil nutrients needed for plants. Intercropping could change the composition of soil microbial communities and increase the activities of some enzymes that promotes nutrients cycling in the soil[7−9]. Moreover, some intercropping patterns can alleviate or control pests that threaten crop growth[10]. As a result, many intercropping patterns could improve the above- and below-ground environment, which are beneficial to crop growth and metabolism[11−14] (Fig. 1). The above-ground part mainly contains the pests and microclimate, such as temperature, humidity, and light intensity. The below-ground part is also called the soil environment, such as soil nutrients, heavy metals, microorganisms, and enzyme activities[15−19] (Fig. 1).

Diversified agroforestry systems have been used in China for over 7,000 years, driven by the economic returns of two or more crops[20]. The wood-tea intercropping pattern has been applied for a long time[21]. Under long-term tea plantation management, different intercropping patterns of tea plantations were established, such as fruit-tea, chestnut-tea and soybean-tea intercropping. Before the 1980s, there was little research on tea plantation intercropping. Until the 2010s, there was basic research on tea plantation intercropping, and most studies focus on the impact of intercropping on the microclimate of tea plantations. Since then, intercropping patterns in tea plantations have developed rapidly, and the contents of intercropping studies are more diversified, such as pests, soil nutrients and microorganisms. Although sufficient studies on intercropping in tea plantations have been reported, many problems and concerns remain to be understood. This review elucidates the effects of intercropping on the above- and below-ground environment of tea plantations and how intercropping affects the growth, yield and quality of tea plants. Finally, we summarize the remaining problems of tea plantation intercropping patterns and provide new insights for tea plantation intercropping.

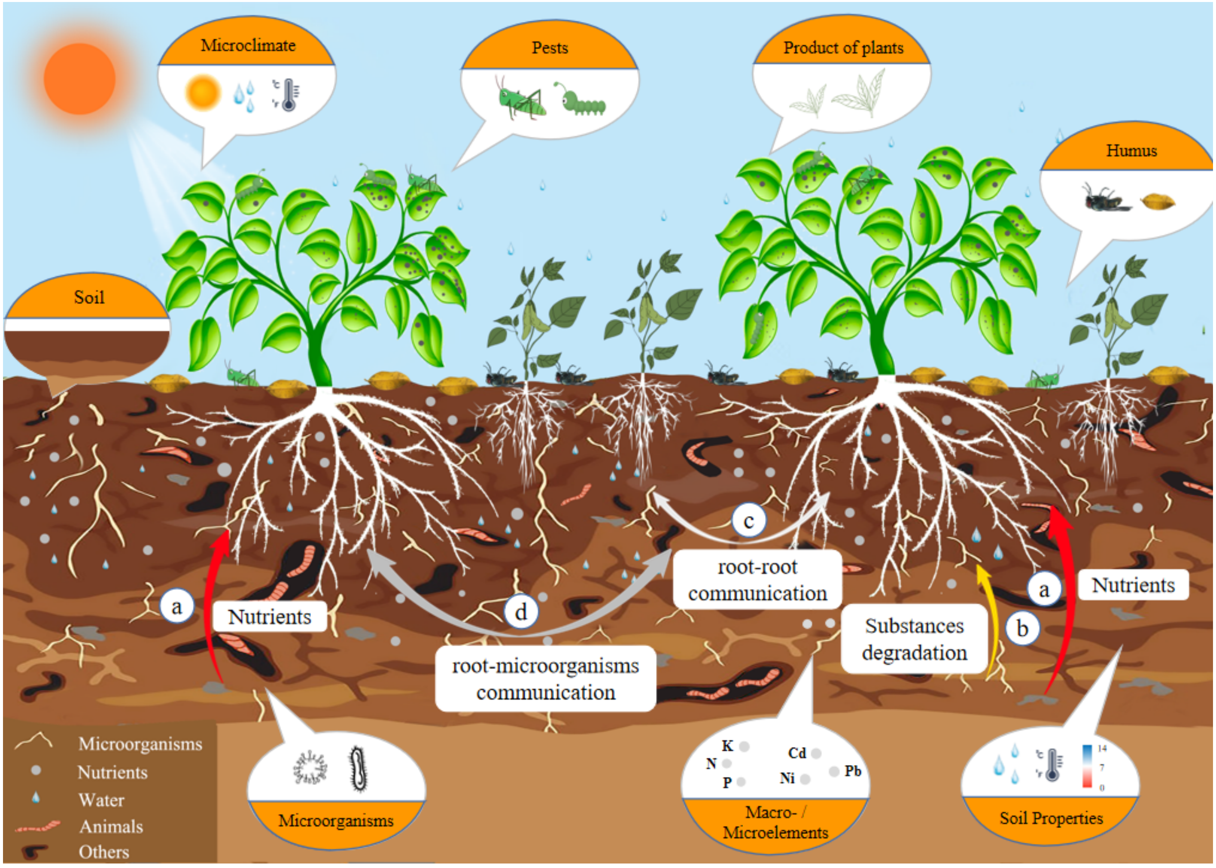

Fig. 1 Interactions between intercropping and host plants. The influence of intercropping on the host plants mainly includes two factors. 1 Above-ground factors: pests and microclimate, such as temperature, humidity and light intensity. 2 Below-ground factors: soil nutrients, enzymes and microorganisms. There are complex material exchanges between host plants, intercropping plants and soil microorganisms. (a) Host plants absorb nutrients from the soil. (b) Soil microorganisms degrade humus in soil. (c) Signal communication between the roots of intercropping plants and the host plants. (d) Signal communication between the roots of host plants and soil microorganisms.

The impact of intercropping on the above-ground environment of tea plantations

Effects of intercropping on temperature of tea plantations

Tea plants originate from tropical rainforests, and they prefer warm and moist environments[22]. The most suitable temperature for the growth of tea plants is 20−25 °C. Tea yield is greatly affected by temperature, and sustained periods of temperature stress result in a reduction in yield. Yield will decrease if tea plants live in an environment where the average monthly temperature is higher than 26.6 °C. At an average monthly temperature of 28 °C, tea yield would decrease by 3.8% for each additional degree[23]. Additionally, if the temperature was below 13 ºC, the growth of tea plants will be inhibited[24]. Therefore, it's important to alleviate the damage caused by temperature stresses in tea plants. A suggestion to alleviate this phenomenon is to select resistant varieties and suitable field management. The key to field management is to reduce the magnitude of temperature changes in tea plantations, mainly including intercropping plants and covering sunshade nets, etc. Intercropping is a more effective agronomic practice to moderate the temperature of tea plantations.

The intercropping woods, fruit trees and other crops in tea plantations can significantly improve the above-ground environment for tea plant growth[15,25]. The branches and leaves of intercropping woody plants can shade tea plants and herbs can cover the soil, so it can reduce the extent of temperature changes. Research shows that intercropping *Vulpia myuros* is similar to black plastic film and rice straw mulch treatments, both of which reduce soil temperature in the summer[15]. White clover-tea intercropping could increase soil temperature under low temperature environments and decrease soil temperature under high temperature environments[26]. Like white clover-tea intercropping, both the fruit-tea, chestnut-tea and soybean-tea intercropping can keep the tea plantation temperature relatively stable[13,16,26].

Almost all studies on intercropping show that it can improve the temperature environment, which is beneficial to tea plant growth. Therefore, intercropping should be recommended in many tea plantations that often suffer from low and high temperature stress. In tea plantations with frequent high and low temperatures, loquat, chestnut and waxberry trees are recommended as tea plantation intercropping plants. Especially, in young tea plantations with low resistance, maize and soybean are recommended as tea plantation intercropping plants.

Effect of intercropping on water environment of tea plantations

The growth, metabolism and yield of tea plants are mainly affected by the available water. Available water in tea plantations mainly includes air humidity and soil water. Drought stress reduces tea yield by 14%−20% and increases tea plant mortality by 6%−19%[27]. Although the annual rainfall in most planting areas meets the water demand for tea plant growth (2,500−3,000 mm per year), uneven distribution of monthly rainfall would inhibit tea plant growth. In China, many planting areas of tea plant have a dry period of more than two months. Therefore, these tea plantations need to be irrigated to alleviate drought stress. Additionally, excessive ambient vapor pressure (> 1.2−2.3 kPa) would inhibit the growth of tea shoots[27]. The excessive transpiration rate of crops would inhibit leaf photosynthesis, leaf growth and shoot elongation[28]. More importantly, most tea plantations are planted with clonal tea plants, and most of the root of the clonal tea plant is located within 30 cm of the soil depth[22]. While it is much shorter than the root of seeding tea plant located at a soil depth of 3.0−5.5 m[29]. Therefore, clonal tea plant is more susceptible to drought stress than seeding tea plant. Due to the uneven distribution of monthly rainfall, the excessive transpiration rate of tea plants and the susceptibility of tea plants to drought stress, water management in tea plantations has always been the focus of tea plantation management.

Field water management includes planting drought-resistant varieties, timely irrigation, timely pruning and field mulching[23]. While intercropping, ground coverings with sunshade nets and straw mulch could lower soil temperature and keep soil water during high temperatures and low rainfall, intercropping plants are more effective in keeping deep soil (15−20 cm) water[15]. The branches and leaves of intercropping plants shade tea plants to reduce ambient temperature and water evaporation. Therefore, intercropping can optimize the tea plantation water environment. For example, intercropping peanut, rubber, *Vulpia myuros and* white clover in tea plantations can reduce soil water loss[15,30−32]. Chestnut-tea and fruit trees (loquat, waxberry, citrus)-tea intercropping lowers air and soil temperatures and increases the air and soil humidity in tea plantations[16,33]. Intercropping can not only improve water environment in tea plantations, but also reduce the risk of soil erosion, especially in the new tea plantation[34]. For example, soybean, peanut and maize (*Zea mays* L.) intercropped in young tea plantations and rubber-tea intercropping could also keep soil water and reduce surface erosion[32,35]. Generally, in areas with uneven rainfall, in order to prevent drought stress or soil erosion, intercropping woody plants is recommended in tea plantations.

There is no doubt that intercropping could improve the water environment of tea plantations. In recent years, harsh climate with continuous high temperature and drought has occurred frequently. Chestnut, citrus and waxberry are recommended to be planted between the rows of tea plants if they are grown in areas with frequent high temperatures and droughts. More importantly, young tea plants with low resistance are more susceptible to drought stress and soil erosion, so soybean and maize are recommended to be intercropped with young tea plants to improve the water environment of tea plantations.

Effects of intercropping on light intensity of tea plantations

Tea plants grow well, and their photosynthetic systems are more effective under moderate shade[22]. Parameters such as photosynthetic light capture, carboxylation and electron transport suggest that the photosynthetic system of tea plants is more efficient under moderate shade. If the light intensity is too high, the net photosynthetic rate of tea will decrease[36]. Tea plants are observed to have an obvious photoinhibition effect under strong sunlight, which slows the growth rate of the tea plant and reduces tea yield. Shading can also reduce leaf temperature by 10−12 °C at noon in summer, and 30%−40% shading is considered the best shading for high-yield tea leaves[27]. Sunshade nets and intercropping patterns are usually used to alleviate the adverse effects of strong light intensity on tea plant growth. As a sustainable cultivation pattern, intercropping is a more efficient light management measure that creates suitable light conditions for tea plant growth.

Intercropping woody plants could shade tea plants, it would significantly reduce the light intensity of tea plantations. Studies on the effect of shading on the tea plants had, for a long time, with most systematic analyses focused on secondary metabolites, such as amino acid, catechin, chlorophyll, lignin and flavonol biosynthesis[37−42]. These metabolites are the key to the formation of good tea quality and the improvement of tea plant stress[41,43]. At present, most of the studies on the effect of shading on tea metabolism are based on the application of black shade net, and it has a short-term and high shading rate (days < 30 and shading rate > 80%)[37,39,40,42,43]. High shading increases the content of most quality related components (Theanine, total amino acid, flavonoids and caffeine), however, shading reduces the abundance of catechin, flavonols and lignin at low and medium shading rates (30%−40%, 50%−60%)[40,41,43]. Although intercropping would also shade tea plants and promote tea plant growth and metabolism, intercropping is not short-term and high shading rate (> 70%). It is different from shading tea plants with a shade net. At present, the effect of different shading rates on the growth and metabolism of tea plants under the intercropping pattern has not been revealed, and only the effect of intercropping on the growth and metabolism of tea plants is concerned[33,44,45]. In the future, it is necessary to reveal the effect of the shading rate of intercropping on the growth and metabolism of tea plants. It is necessary to identify the optimal shading rate of intercropping and the optimal planting density of intercropping plants in tea plantations.

Effects of intercropping on pests in tea plantations

Pests are an essential part of the global ecosystem. They however reduce tea yield by about 15%−20% and cause huge economic losses[46]. Appropriate field management and control measures could decrease the loss of tea yield caused by pests. Pests can be controlled by a comprehensive approach including physical, chemical and biological technologies[47−49]. Although chemical and biological techniques are the main techniques for controlling pests in tea plantations, intercropping should be used as an environmental-friendly technique for controlling pests. Unlike chemicals and botanical insecticides, intercropping does not kill pests directly, it only prevents or alleviates certain pests without pollution[11,50]. Compared with chemical pesticide-treated tea plantation, intercropping can significantly reduce the number of pests, increase the number of natural enemies of pests and improve the quality of tea (more aroma substances)[51]. How could intercropping affect the incidence of pests in tea plantations? On the one hand, odor released from aromatic plants could repel some pests[52], on the other hand, intercropping increases the biodiversity of tea plantations, especially increasing the abundance of natural enemies of pests, which would control the pests[11,53].

Although there are many kinds of common pests, green leafhopper (*Empoasca onukii* Matsuda) is the most concerning. Many studies showed that intercropping patterns efficiently repel green leafhoppers and increase the abundance of natural enemies (Table 1). Intercropping aromatic plants (*Lavandula pinnata* L., *Tagetes erecta* and *Leonurus Artemisia*) in tea plantations could effectively repel leafhoppers by volatile compounds (alpha-pinene, 1,8-cineole, thymol anisole, etc.)[52−54]. Additionally, some intercropping plants (*Rosmarinus officinalis* L., *Catsia tora* and *Paspalum notatum*) increase the abundance of natural enemies (spiders, ladybirds and coccinellids) of leafhoppers to control them[17,52,55]. Some studies reveal the impact of intercropping on other pests in tea plantations. Intercropping multiple plants (*Chamaecrista rotundifolia*, red bean, maize *and Rosmarinus officinalis*) would effectively control herbivorous pests in tea plantations[56−58]. However, not all intercropping plants could effectively control pests. *Chamaecrista rotundifolia*-tea and *Paspalum notatum*-tea intercropping had little effect on the abundance of natural enemies of pests in tea plantations[50]. Although motherwort-tea intercropping could increase the abundance of natural enemies of *Orius sauteri*, tea plants may became more susceptible to aphids and powdery mildew[57]. As a result, it is necessary to choose suitable intercropping plants according to pests in the tea plantation.

Most studies have focused on intercropping plants to repel pests (Table 1). The volatile components released by these plants should be fully utilized and they could be made into botanical repellents. These botanical repellents are derived from plants and they do not pollute the tea leaves and environment, so it will be widely used in agricultural production. Additionally, it is only reported that intercropping could effectively control several pests, but other common pests (*Polyphagotarsonemus latus*, *Aleurocanthus spiniferus*) have not been studied. Therefore, the effect of intercropping on other pests should be revealed and more botanical repellents need to be exploited in the future, which lay a foundation to control pests in ecological tea plantations.

Influence of intercropping on the below-ground environment of tea plantations

Tea plants grow in soil, and soil nutrients promote tea plant growth and development. Soil available nutrients are easily affected by plant diversity, soil microbial communities, soil properties, such as soil pH, texture, and temperature[61−64]. Therefore, the soil environment of a tea plantation is an essential factor that affects tea yield. Intercropping could change the below-ground environment. For example, intercropping improves soil nutrients, moisture and temperature, reduces the content of heavy metals and changes soil enzyme activities and microbial community[13,16,44,65−67].

Effects of intercropping on soil nutrients in tea plantations

Intercropping is a recommended planting pattern that plays an effective role in increasing and maintaining long-term productivity and sustainability. Soil fertility will be improved, soil acidification will be alleviated, thus intercropping could reduce the input of fertilizers[2,18]. Intercropping could improve soil nutrients in tea plantations mainly including two factors (Table 2). On the one hand, intercropping increases topsoil and subsoil organic matter, and promotes the release and recycling of soil nutrients[68]. Many available nutrients in soil are positively affected by intercropping, such as total nitrogen (TN), available nitrogen (AN), available potassium (AK), total phosphorus (TP), available phosphorus (AP), and soil organic matter (SOM.[13,16,18]. On the other hand, intercropping changes soil microbial abundance and enzyme activities[9,69]. Intercropping could increase some soil enzyme activities and the abundance of beneficial microorganisms that could promote nutrient cycling.

The effects of intercropping on various kinds of nutrients are different. AP, AK and SOM increased significantly compared to monoculture under osmanthus-michelia-tea, peanut-tea, walnut-tea and *Vulpia myuros*-tea intercropping patterns[9,14,15]. Especially, *Vulpia myuros*-tea and walnut-tea intercropping is

Table 1. Effects of different intercropping patterns on pests in tea plantations.

Tea plantation intercropping plant(s)	Pest(s) and effect	Volatiles/predators	Reference(s)
Flemingia macrophylla	Leafhoppers are attracted	Volatiles (*cis*-3-hexen-1-ol, *cis*-3-hexenyl acetate, nonanal and alpha-farnesene)	[54]
Lavandula pinnata L., *Corymbia citriodora* (Hook.), *Tagetes erecta*, *Leonurus Artemisia*	Leafhoppers are repelled	Volatiles (alpha-pinene, 1,8-cineole, thymol anisole, thymol, p-cymene, limonene and camphor)	[52–54]
Rosmarinus officinalis L., *Catsia tora* and *Paspalum notatum*	Leafhoppers are controlled	predators (spiders, ladybirds, coccinellids, and lacewings, *Anystis baccarum*)	[17, 52, 55]
Chamaecrista rotundifolia	Herbivorous beetles, *Thysanoptera* or *Geometridae* are controlled	Predators (*Serangium japonicum*, *Pharoscymnus taoi*, *Cryptogonus postimedialis* or parasitoids)	[11, 56]
Mentha haplocalyx	Green plant bugs are repelled	Volatiles (unknown)	[53]
Red bean	Leafhoppers and thrips are controlled	Predators (*Orius sauteri*)	[57]
Rosmarinus officinalis	*Ectropis obliqua* are repelled	Volatiles (Beta-myrcene, Gamma-terpinene, (R)-(−)- linalool, (S)-(−)-cis-verbenol, (R)-(+)-camphor, and (S)-(−)-Verbenone)	[59]
Maize	Leafhoppers and *Trialeurodes vaporariorum* are controlled	Volatiles (unknown)	[58]
Acacia confusa Merr. trees	*Hemiptera*, *Lepidoptera*, and *Coleoptera* are controlled	Predators (*Araneida, Hymenoptera, Hemiptera*)	[60]

Table 2. Effects of different intercropping patterns on soil nutrients.

Tea plantation intercropping plant(s)	Nutrients increased in intercropping patterns	Reference(s)
Soybean	Ammonium N, Nitrate N, AP, OM, AK (flowering–podding or mature period of soybean)	[13]
Chestnut	SOM, N, P and K	[18]
Stropharia rugosoannulata	SOM, TN and AN	[68]
Osmanthus and Michelia	TN, TK, AN, AP and SOM	[14]
Loquat or citrus or waxberry	AN, AP, AK and SOM (loquat) and AP, AK and SOM (waxberry) and AN, AP and AK (citrus) in top-, sub- and bottom-soil	[16]
Peanut	TP, TK, AP and AK in top-, sub- and bottom-soil	[9]
Walnut	AN, AP, AK and SOM	[69]
Vulpia myuros	SOM, TN, alkali-hydrolyzed N, AP and AK	[15]

over 50% in top-soil. However, TN, TK and TP didn't show much difference. Additionally, intercropping has different effects on nutrients in different soil layers. Overall, the magnitude of soil nutrient changes in most intercropping tea plantations increased with soil depth[9,16,18]. For example, under peanut-tea intercropping pattern, available phosphorus (AP) was 52.9%, 26.56% and 61.1% higher than the monoculture and available potassium (AK) was 11.1%, 43.06% and 46.79% higher than the monoculture in 10–20 cm, 20–30 cm, and 30–40 cm soil layers respectively[9]. Intercropping improves air environment and reduces greenhouse gas emissions[70,71]. For example, sorghum-tea intercropping reduces nitrous oxide (N_2O) emissions while increasing the available nitrogen content in soil, and thus improves the soil nutrients for the growth of tea plants[31,72].

Intercropping is a more suitable planting pattern than monoculture. Intercropping reduces the input of chemical fertilizers, which reduces adverse effects on soils. Although the intercropping could reduce the input of chemical fertilizers, it does not completely abandon chemical fertilizers. Intercropping patterns have different effects on various nutrients, the appropriate proportion of fertilizer should be applied based on soil nutrients. Therefore, the amount of externally input chemical fertilizers under different intercropping patterns should be revealed.

Effects of intercropping on soil enzyme activities in tea plantations

Soil enzymes are important biocatalysts in soil. They could catalyze the decomposition of animals, plants and microorganisms in the soil, promote nutrient recycling in the soil, and ultimately increase the nutrients in the soil[73]. Soil enzymes such as dehydrogenase, catalase, invertase, and urease degrade plant and animal debris in the soil, and the nutrients that are subsequently released into the soil, which are available to plants[9]. Soil enzymes are closely related to soil nutrient cycling and soil health, so they could be indicators of soil health[9]. The hydrolysis of sucrose by invertase promotes the soil carbon cycle and peroxidase activity is inversely correlated with the availability of inorganic nitrogen[74,75]. Soil enzyme activities are closely related to microorganisms and nutrients, so it is necessary to reveal the changes of soil enzyme activities under different tea plantation intercropping patterns.

Intercropping increases the activity of various enzymes. In the chestnut-tea intercropping tea plantation, the activities of catalase, urease, dehydrogenase, invertase, and polyphenol oxidase were improved[18]. Intercropping peanuts or walnut in tea plantation increased the activities of acid phosphatase and protease in soil[9,69]. Invertase, urease, acid phosphatase and peroxidase promote carbon, phosphorous and nitrogen cycling in soil. Therefore, compared with monoculture, soil N, P and K content increased in peanut-tea, chestnut-tea and walnut-tea intercropping tea plantations[9,12,69]. Additionally, soil enzyme activities are different in response to different intercropping patterns. The acid phosphatase activity was significantly increased in peanut-tea intercropping patterns, while the catalase and urease activities were significantly increased in chestnut-tea intercropping patterns[9,12]. This result is consistent with soil nutrients in different intercropping patterns. More importantly, soil enzyme activities were also strongly affected by soil temperature, they are generally most active in spring and early summer[9]. Therefore, soil enzymes should be maintained at high activity to increase soil nutrients.

Soil enzymes promote soil nutrient cycling and increase soil nutrients, and soil enzyme activities are greatly affected by soil temperature. Therefore, field mulching and intercropping are recommended to maintain soil temperature and enzyme activities. Additionally, intercropping patterns have different effects on the enzyme activities that promote nutrient cycling, so more attention should be paid to the effects of different intercropping patterns on soil enzyme activities in the future.

Effects of intercropping on soil microorganisms in tea plantations

Tea plantation soil contains a variety of microorganisms, among which bacteria and fungi play an important role in maintaining soil ecological functions[65]. Soil microorganisms could accelerate soil nutrient cycling, litter degradation and decrease carbon emissions[65]. However, soil microbial community structure is extremely fragile, and easily affected by cultivation patterns, soil properties and plant type[14,61,73]. Planting patterns significantly change soil microbial abundance, composition and diversity. Many studies have shown that the alpha diversity of soil bacterial and fungal communities, and the beta diversity and abundance of bacterial communities in intercropping patterns are higher compared to monoculture[14,58,65,76]. Soil nutrients could change microbial community diversity and abundance in soil, and vice versa[65]. Therefore, soil microorganisms affected by many factors could change soil nutrients.

Tea plantation soil contains many kinds of microorganisms. In tea plantation soil, *Acidobacteria*, *Actinobacteria*, *Chlorophyte* and *Proteobacteria* are the most common bacterial taxa at the phylum-level[76]. The *Ascomycota* and *Basidiomycota* are the most common fungal taxa at the phylum-level[77]. Intercropping increases the abundance of soil beneficial microbial such as *Proteobacteria, Firmicutes, Ascomycota* and *Mortierellomycota*[14,58,69,76]. These soil beneficial microorganisms promote soil nutrient cycling or increase plant resistance[68,76].

Additionally, intercropping changes the structure of bacterial communities in tea plantation soils. Soil microorganisms shifted from oligotrophy (*Chloroflexi, Acidobacteria* and the candidate phylum WPS-2) to copiotrophy (*Proteobacteria* and *Bacteroidetes*) in soybean-tea intercropping patterns[76]. Therefore, there is a significant correlation between soil microorganisms and nutrients. Soil nutrients (SOM, AP and AK) were positively correlated with beneficial bacterial communities including *Proteobacteria*, *Firmicutes* and *Bacteroidetes*[12,14].

Although intercropping increases the abundance of beneficial microorganisms in tea plantation soil, the complex relationship between soil nutrients and microbial abundance and diversity has not been fully revealed. More importantly, intercropping increases the abundance of beneficial microorganisms[68,76]. Therefore, these beneficial bacteria and fungi should be inoculated into the tea plantation soil, which can promote the nutrient cycle of tea plantation soil and improve plant resistance. Additionally, the soil microorganisms in the intercropping tea plantations should be studied deeply, and their specific identities should be revealed.

Effects of tea plantation intercropping on soil heavy metals

The accumulation, toxicity and non-degradability of heavy metals in agricultural soils have attracted worldwide attention. Plants absorb most nutrients and heavy metals from soil. If tea plantation soil was polluted by heavy metals, tea plants will absorb and accumulate them, affecting tea quality and health[78]. The uptake of soil heavy metals by plants is mainly influenced by pH, soil organic matter, heavy metal content, and texture[79]. Soil heavy metals remediation methods include microbial and plant remediation, ionization deposition, soil replacement and redox deposition[80]. Intercropping is one of the important measures to remediate mild heavy metal pollution in tea plantation soil. Some plants with strong accumulation of heavy metals could absorb them from polluted soil and transport and accumulate them in the above-ground organs of plants. Therefore, hyperaccumulators should be recommended as intercropping plants if the tea plantation soil is lightly contaminated with heavy metals.

Although the ability of intercropping plants to absorb tea plantation soil heavy metals has not been fully revealed, it is well known that intercropping some plants could uptake soil heavy metals. For example, Compared with monoculture, tomato, maize and clover intercropped with host plants significantly would reduce the content of Pb, Cr and Cu in soil[81]. Heavy metals are closely related to microorganisms, nutrients, pH and tea quality[82,83]. Under different fruit-tea intercropping (loquat, bayberry, citrus) patterns, the content of soil heavy metals (Cd, Ni, Cr, Mn) were negatively correlated with the content of soil nutrients (AN, TN, AK, AP and TK) and tea quality components (caffeine, amino acid, catechins). Additionally, there are obvious differences in the uptake or accumulation of heavy metals by different plants. The content of heavy metals in the citrus-tea intercropping soil were lower than loquat-tea and waxberry-tea intercropping soil. At the same time, the tea quality of citrus-tea intercropping is better than the other two intercropping patterns[16]. Therefore, it is very important to choose suitable intercropping plants. As is well known, *Thlaspi rave service* L., *Arthrocnemum macrostachyum* and *Calendula officinalis* as hyperaccumulator plants should be used to alleviate mild heavy metal stress in tea plantation soil[80]. For example, *Arthrocnemum macrostachyum* could enrich Fe, As and Mn[84]. Therefore, it is recommended to be intercropped with host plants for the remediation of mild heavy metal-contaminated soils.

Although the soil is seriously polluted by heavy metals and cannot be remediated by intercropping hyperaccumulator plants, it is still recommended to remediate soil by intercropping hyperaccumulator plants in tea plantations with mild to heavy metal pollution. Therefore, we need to reveal the enrichment ability of hyperaccumulator plants for different heavy metals, which will lay a foundation for intercropping plants to alleviate heavy metal stress in tea plantations.

Effects of intercropping on tea plant growth, yield and quality

As is well known, the growth and development of tea plants are influenced by many environmental factors. Intercropping would change the environment for the growth of tea plants, which includes above- and below-ground environments. At the same time, these environmental factors could affect the metabolism of tea plants, which are closely related to the growth and quality of tea plants. Therefore, the effect of intercropping on plant growth and metabolism is a complex mechanism, which is regulated by a variety of environmental factors.

Effects of intercropping on the growth and yield of tea plants

Tea plantation microclimate, soil nutrients, soil microorganisms and pests are closely related to tea plant growth and yield. Some of the relationships between them have been revealed. Intercropping changes light, temperature and water conditions, which are necessary conditions for tea plants to grow. Tea plants are suitable for groth in a moderate temperature (20–25 °C), humid (rainfall is 2,500–3,000 mm per year) and moderate shade environment. However, the environment of monoculture tea plantations cannot meet this condition, which will not be beneficial to the growth and development of tea plants. Woody plants and herbs could protect tea plantation environment. Therefore, herb-tea (e.g., soybean, white clover and maize) and woody plant-tea (e.g., chestnut, citrus and waxberry) intercropping could significantly improve temperature, water and light in tea plantations. Intercropping could reduce the magnitude of temperature, water and light changes in tea plantations, and it could obviously alleviate the stress of temperature, water and strong light, which is beneficial to tea plant growth and yield[13,16,26,32,33,44,45]. Additionally, the number of pests is negatively correlated with tea yield. Intercropping is an environmental-friendly pest control measure. Intercropping a variety of aromatic plants (e.g., *Lavandula pinnata* L., *Tagetes erecta* and maize) could increase the abundance of natural enemies of pests (e.g., spider, coccinellids and lacewings), reduce the abundance of pests and repel pests (e.g., green leafhopper, *Empoasca onukii* and *Apolygus lucorum*) in tea plantations, which could promote tea plant growth and increase tea yield[17,52,53,85].

Tea plants grow in soil, so soil nutrients are crucial for the growth of tea plants. Soil nutrients are affected by soil microorganisms, enzyme activities and soil properties. Intercropping increases the content of some nutrients (C, N, P or SOM) in the tea plantation soil[9,18,69]. Walnut-tea, peanut-tea and soybean-tea intercropping could increase the abundance of some soil beneficial microorganisms (e.g., *Proteobacteria, Firmicutes,* and *Ascomycota*) and the activities of soil enzymes (e.g., invertase, urease, acid phosphatase and peroxidase), which could promote the degradation of animal and plant debris and soil C, N and P cycling[14,58,69,76]. Chestnut-tea, waxberry-tea and citrus-tea intercropping could alleviate soil acidification and heavy metal stress, so they could promote tea plant growth[86,87]. As a result, legumes, chestnut, walnut and aromatic plants are suitable as intercropping plants that are beneficial to tea plant growth and high-yield tea leaves.

Effects of intercropping on the quality of tea

These components (e.g., amino acids, catechins and caffeine, etc.) related to tea quality are synthesized by the metabolism of tea plants. The metabolism of tea plants are affected by microclimate, soil nutrients, and microorganisms. Intercropping could improve the microclimate, soil nutrients and soil properties of tea plantations, which promote the synthesis of tea quality components. Therefore, intercropping can positively affect tea quality.

The above and below-ground environment of tea plantation determines tea quality. Appropriate temperature, light, water and soil environment are the basis for the formation of high-quality tea. When tea plants are damaged by high temperature, low temperature, drought, pests or strong light, the metabolic activities of tea plants are inhibited[33,37,38,51,88]. Appropriate soil nutrients that are determined by fertilizer input, soil enzymes and microorganisms are the basis for the growth and metabolism of tea plants[9,14,69,76]. Intercropping improves temperature, water and light conditions in tea plantations and increases soil nutrients, the abundance of soil beneficial microorganisms and the activities of soil enzymes, which could promote the synthesis and metabolism of tea quality components (amino acids, catechins, caffeine, and aroma components)[13,16,33,42,45,51,69]. Amino acids, polyphenols and caffeine are higher, while catechins were lower in soybean-, chestnut-, fruit trees- and *Vulpia myuros*-tea intercropping than monoculture[9,13,15,16,18,44]. Additionally, chestnut-tea intercropping promotes biosynthesis of volatiles (phenylpropanoid, monoterpenoid, and sesquiterpenoid), flavone and flavonol in tea leaves[33,45]. Therefore, intercropping improves the environment of tea plantations and promotes the synthesis and accumulation of tea quality components, which improves tea quality.

Conclusions and outlook

Intercropping is a green and sustainable planting pattern that promotes tea plant growth and development. Intercropping would improve the environment in which the tea plant grows, both above- and below-ground. Intercropping reduces the magnitude of temperature changes, preserves soil water, shades tea plants and control pests, which maintains a suitable above-ground environment for tea plants. Therefore, the growth and metabolism of tea plants could be promoted under tea plantation intercropping patterns. Additionally, intercropping could also improve the below-ground environment. Under intercropping patterns, soil nutrients, properties, enzyme activities and beneficial microbial abundance were improved, and heavy metal stress was alleviated. Among these soil components, soil nutrients are the key. On the one hand, most nutrients needed for plant growth and metabolism are absorbed from the soil. On the other hand, soil microorganisms and enzyme activities could degrade litter and promote soil nutrient cycling, and heavy metals are negatively related to soil nutrients. As a result, intercropping increases soil nutrients that promote the growth and development of tea plants.

Although most research results reveal that intercropping is an efficient and environmentally-friendly planting pattern that promotes the growth and development of tea plants and improves tea yield and quality, there are still many problems that need to be solved.

1. Intercropping could improve light, temperature and water conditions in tea plantations, the effects of different intercropping plants and intercropping densities on the tea plantation environment, tea plant growth, tea quality and yield have not been revealed. Suitable intercropping plants and the most suitable planting density need to be explored in different tea plantations.

2. Volatiles released by intercropping aromatic plants could repel pests. There are a series of problems that need to be solved. Which pests are repelled by these volatiles? What is the mechanism by which these volatiles repel pests? More importantly, these volatiles should be made into environmentally-friendly pest repellants.

3. Intercropping could increase the soil nutrients (N, P and K) in tea plantations. However, chemical fertilizers still need to be added to intercropping tea plantations. The amount of fertilizer and the proportion of N, P and K under different intercropping patterns should be revealed.

4. Soil enzymes could promote soil nutrient cycling, but enzyme activities are greatly affected by temperature. It is necessary to reveal the suitable soil temperature that maintains high activity of soil enzyme. The effects of intercropping plant types and planting density on enzyme activities need to be revealed.

5. Many beneficial microorganisms in intercropping tea plantation soil could degrade litter and promote soil nutrient cycling. The identity of these beneficial microorganisms that increase soil nutrients needs to be further revealed and they should be inoculated into the tea plantation soil.

6. At present, there are few studies on soil heavy metals in intercropping tea plantations. The effect of intercropping hyperaccumulator plant on heavy metals in tea plantation soil and the uptake and enrichment of different heavy metals by hyperaccumulator plants need to be revealed.

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Conflict of interest

The authors declare that they have no conflict of interest.

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