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REVIEW

A review of research progress on continuous cropping obstacles

Kunguang WANG[1], Qiaofang LU[1], Zhechao DOU[1], Zhiguang CHI[1], Dongming CUI[1], Jing MA[1], Guowei WANG[2], Jialing KUANG[3], Nanqi WANG[1], Yuanmei ZUO (✉)[1]

1 College of Resources and Environmental Sciences, State Key Laboratory of Nutrient Use and Management, National Academy of Agriculture Green Development, China Agricultural University, Beijing 100193, China.
2 College of Resources and Environmental Sciences, Southwest University, Chongqing 400715, China.
3 Yunnan ICL YTH Phosphate Research and Technology Co., Ltd., Kunming 650228, China.

KEYWORDS

Continuous cropping obstacles, rhizosphere regulation, soil microecological environment

HIGHLIGHTS

- Continuous cropping obstacles (CCOs) cause, on average, 22% reduction in crop production, seriously threatening sustainable agricultural development.
- Changes in the soil ecological environment are an essential and easily overlooked cause of CCOs.
- Studying CCOs from the perspective of the soil microbial food web may provide new approaches for explaining the formation mechanism of CCOs and controlling soilborne pathogens.
- Not all continuous cropping systems have CCOs, and some systems may enrich beneficial microorganisms to form healthy and disease-suppressive soil.

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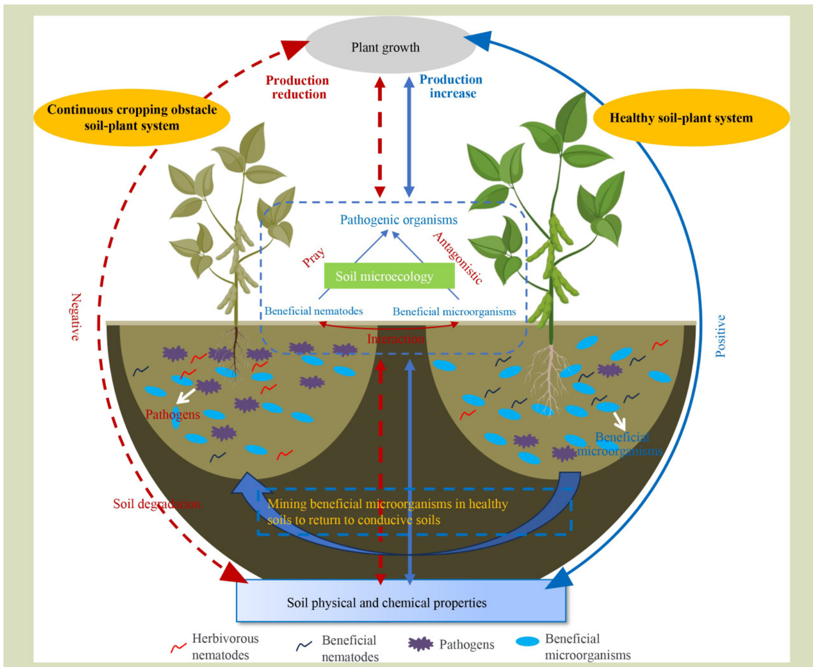
Correspondence: zuoym@cau.edu.cn

GRAPHICAL ABSTRACT



ABSTRACT

Due to the increasing global population and limited land resources, continuous cropping has become common. However, after a few years of continuous cropping, obstacles often arise that cause soil degeneration, decreased crop yield and quality, and increased disease incidence, resulting in significant economic losses. It is essential to understand the causes and mitigation mechanisms of continuous cropping obstacles (CCOs) and then develop appropriate methods to overcome them. This review systematically summarizes the causes and mitigation measures of soil degradation in continuous cropping through a meta-analysis. It was concluded that not all continuous cropping systems are prone to CCOs. Therefore, it is necessary to grasp the principles governing the occurrence of diseases caused by soilborne pathogens in different cropping systems, consider plant–soil-organisms interactions as a system, scientifically regulate the physical and chemical properties of soils from a systems perspective, and then regulate the structure of microbial food webs in the soil to achieve a reduction in diseases caused by soilborne pathogens and increase crop yield ultimately. This review provides reference data and guidance for addressing this fundamental problem.

1 Introduction

Continuous cropping obstacles (CCOs) refer to the phenomenon that the same crop or its related species are continuously planted on the same plot, and even under normal management conditions, the yield and quality of products are still reduced, and the diseases and insect pests become serious[1–3]. CCOs are caused by multiple biotic and abiotic factors, such as soil degradation, plant autotoxicity and changes in the soil biological community[4]. Of these, rhizosphere microecological imbalance is the most crucial cause of CCOs[5]. Soil microbial communities consist of various groups, such as bacteria, fungi, protozoa and nematodes. The relationships between these organisms constitute the soil microbial food web that is vital for soil health, nutrient cycling and agricultural productivity[6,7]. Currently, most studies on continuous cropping focus on single organisms, neglecting interactions between multiple organisms in soil food webs, which limits in-depth exploration of soil biological communities. Through a combination of meta-analysis and a summary of current research, we analyze the causes of CCOs and highlight the potential of soil food webs to evaluate them. Also, this review summarizes the incidence patterns of soilborne pathogens, and the disease they cause, in continuous cropping soils. It is important to note that not all continuous cropping systems are affected by to soilborne pathogens, and not all disease caused by soilborne pathogens are severe every year[8–12]. CCOs must be targeted based on a clear understanding of the principles governing their occurrence in different continuous cropping systems from the perspective of plant–soil-organisms interaction system. Our results provide a scientific basis for improving soil health and sustainable agricultural production.

2 Materials and methods

2.1 Data screening

The meta-analysis data set was compiled from peer-reviewed papers published before May 2023 and obtained from the Science Citation Index Expanded database of the Web of Science. The literature search terms used in this study were (TS = (“continuous cropping” OR “succession cropping” OR “monocropping”)) AND (TS = (microbiome OR microbiota OR bacteria OR bacterial OR fungi OR fungal OR nematode OR “physicochemical propert*” OR “physical and chemical propert*”)). To accurately screen for useful literature, we set a number of selection criteria: the research must consist of field or pot experiments from continuous cropping soils, excluding model simulations; it must involve continuous cropping age series, excluding soils for single-year cropping; at least one of the response variables (physical and chemical properties of soil or soil microbial community) had to be reported; only data obtained using high-throughput sequencing methods were collected, excluding data obtained using methods such as phospholipid fatty acid, denaturing gradient gel electrophoresis, or terminal restriction fragment-length polymorphism analyses; The microorganisms must be soil bacteria or fungi as a whole community, excluding studies that targeted specific groups of microorganisms such as mycorrhizal fungi or anaerobic bacteria; finally, definite replicate numbers were required (Fig. S1). Based on these criteria, we identified 112 publications, including a total of 1623 observations. Physical and chemical property indicators, such as soil pH, electrical conductivity, and total nitrogen, and soil microbial community indicators, such as the Chao1 and beta diversity indices, were recorded for each site described in these publications.

2.2 Data analyses

The natural logarithm of the response ratio (RR) was selected as the effect size to indicate the effects of continuous cropping on physical and chemical property indicators (e.g., pH, electrical conductivity and total nitrogen content) and soil microbial community indicators (e.g., Chao1, abundance-based coverage, and Shannon diversity and beta diversity indices), as[13]:

$$\mathrm{RR} = \ln\left(\frac{X_t}{X_c}\right) = \ln X_t - \ln X_c \qquad (1)$$

where, X_t and X_c are the mean values of each indicator group, under continuous cropping treatment (t) and control (c) conditions, respectively. The variance (v) was calculated as:

$$v = \frac{S_t^2}{n_t X_t^2} + \frac{S_c^2}{n_c X_c^2} \quad (2)$$

where, n_t and n_c are the sample sizes, S_t and S_c are the standard deviation of means under continuous cropping treatment (t) and control (c) conditions, respectively.

The percentage change (E) of the RR was calculated as:

$$\mathrm{E} = \left(\mathrm{e}^{\mathrm{RR}} - 1\right) \times 100\% \quad (3)$$

Meta-analysis was conducted using the *rma.mv* function of the R package "metafor"[14] to assess the overall effects of continuous cropping on physical and chemical properties and the soil microbial community. To account for the dependence of multiple observations in the same study, we included the study and site as random factors in the meta-analysis model. We considered the estimated parameter to be significant when the 95% CI did not overlap with zero[15]. Linear fitting was performed for the relationship between the RR of yield/pH and continuous cropping years. All graphs were drawn using R packages "meta"[16] and "ggplot2"[17].

We collected soil microbial community structure and beta diversity data from two-dimensional ordination plots. Specifically, we extracted values from scatter plots in each two-dimensional ordination plot of treatment and control, thereby achieving a meta-analysis (based on one-dimensional data) of community data from two-dimensional ordination plots. The methods followed were as previously described in detail[18]. The ordination plots included non-metric multidimensional scaling, principal component analysis, principal correspondence analysis and redundancy analysis. The symbols and colors used in the figures follow those of previous publications[10,19].

3 Current status of CCOs research

Given the threat of CCOs to global food security, research attention to these issues has gradually increased in recent years and has shown rapid progress. In a preliminary search of the Science Citation Index Expanded database, we found that the number of publications and citations related to continuous cropping has increased exponentially since 2000 (Fig. 1(a)). Such studies involve agronomy, environmental science, ecology and other major research fields (Fig. 1(b)). According to the global distribution of research related to continuous cropping, about 77% of the research has originated from China (Fig. 1(c)). Therefore, we used China as an example to conduct a follow-up analysis.

Continuous cropping has been applied to the cultivation of grain crops (rice and wheat), vegetable crops (tomato and cucumber), economic crops (tobacco and peanut) and medicinal crops (*Panax ginseng* and *P. notoginseng*) (Fig. 2(c)). Among all continuous cropping crops, economic, medicinal, food, vegetable, fruit and forage crops account for about 31%, 23%, 18%, 18%, 6% and 3%, respectively (Fig. 2(b)). CCOs have been reported in almost all provinces in China (Fig. 2(a)). Notably, the area of heavily affected continuously cropped land in China exceeds 10%, more than 20% of which is located in large-scale farming areas; crop losses reach 20% to 80%, and the associated economic losses will approach tens of billions of yuan[20]. Thus, CCOs have become one of the most significant limiting factors restricting sustainable agricultural development in China.

4 Mechanisms underlying CCOs

CCOs result from the joint interaction of plants, soil and soil organisms. It is commonly believed that changes in soil physical and chemical properties, variations in soil ecological environment, and plant autotoxicity are the leading causes of CCOs[1,3]. These three mechanisms usually interact and jointly limit grain production capacity. Bibliometric analysis found that changes in soil physical and chemical properties, plant autotoxicity and variations in soil ecological environment accounted for 34%, 22% and 44% in CCO soil, respectively (Fig. 2(d))[5]. Therefore, biological factors may be the most crucial cause of CCOs.

4.1 Changes in soil physicochemical properties

Long-term continuous cropping and the excessive input of physiologically acidic fertilizers can easily lead to soil acidification. Excessive mineral fertilizer input reduces the average soil pH of Chinese fields by approximately 0.13–0.8[21]. Our meta-analysis results preliminarily support this assessment. Research indicate that compared with non-continuous cropping, continuous cropping reduced soil pH in China by 8% on average (Fig. 3(b)) and that soil acidification will become increasingly severe as the duration of continuous cropping is extended (Fig. 3(c)). Soil acidification directly affects crop growth by affecting the content of metal ions in the soil, causing iron toxicity, aluminum toxicity and cadmium pollution[22–26]; inhibits the absorption of nutrients such as calcium, magnesium and phosphorus by crops[27], and even indirectly limits increases in crop productivity by promoting the proliferation of acidophilic soilborne pathogens such as cyst nematodes, and the Fusarium wilt and bacterial wilt pathogens[28,29]. We also found that continuous cropping can

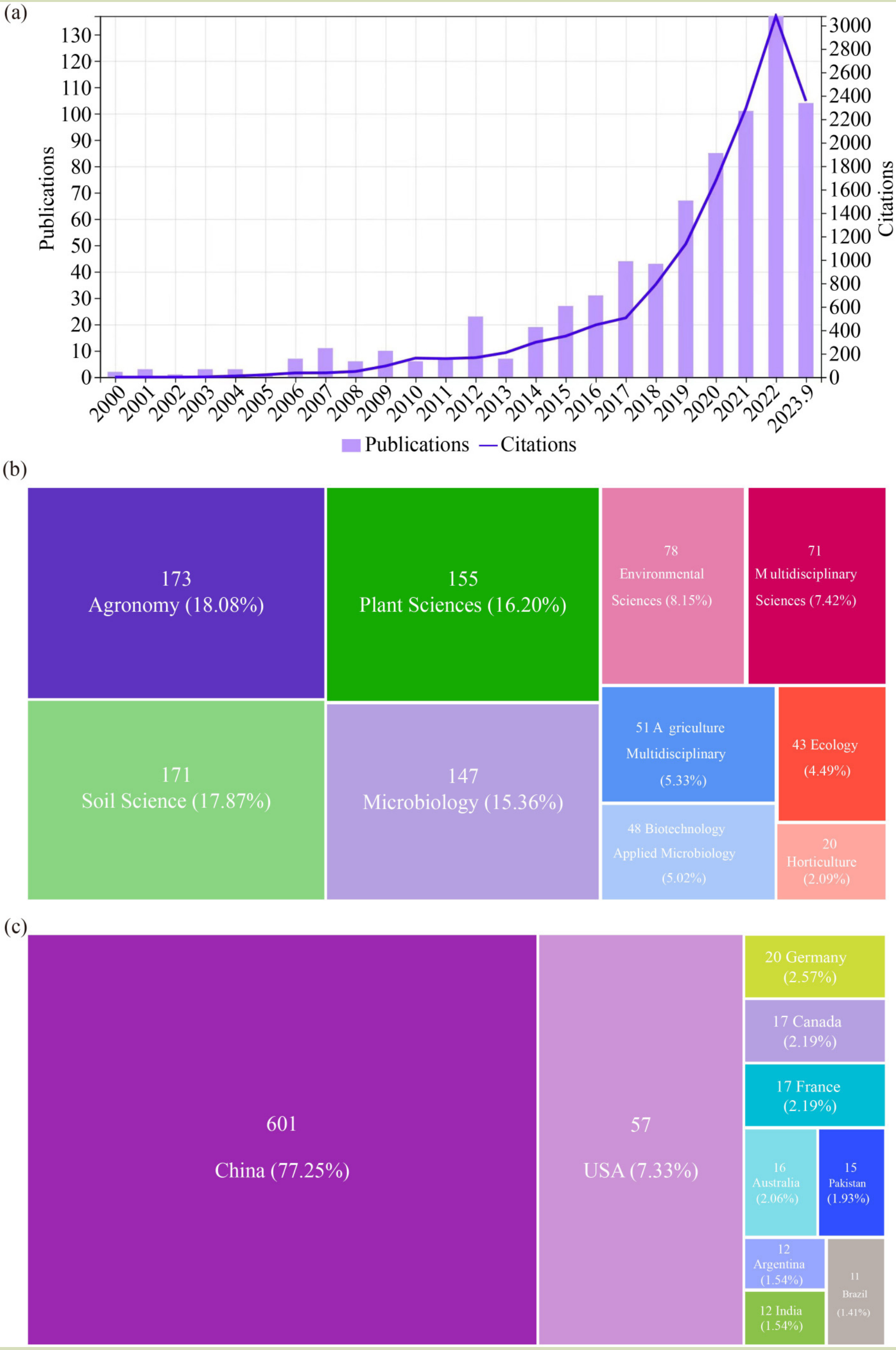


Fig. 1 Overview of research on CCOs: (a) numbers of articles and citations related to CCOs published over time; (b) main research fields related to continuous cropping; and (c) proportion of studies on continuous cropping in different countries.

both acidify and alkalize soil; the impact of continuous cropping on soil pH leads to one of these two extremes (Fig. 3(b)), which may be related to different fertilization management processes and the accumulation of specific root exudates during continuous cropping of plants. Studies have shown that the roots of plants that have been long-term irrigated with ammonia nitrogen fertilizer will secrete H^+ to acidify the rhizosphere[30]. In contrast, the roots of plants with long-term application of nitrate nitrogen fertilizer will secrete OH^- to alkalize the rhizosphere[31]. Another manifestation of the changes in soil physicochemical properties is the stoichiometric imbalance between plants and soil. It was

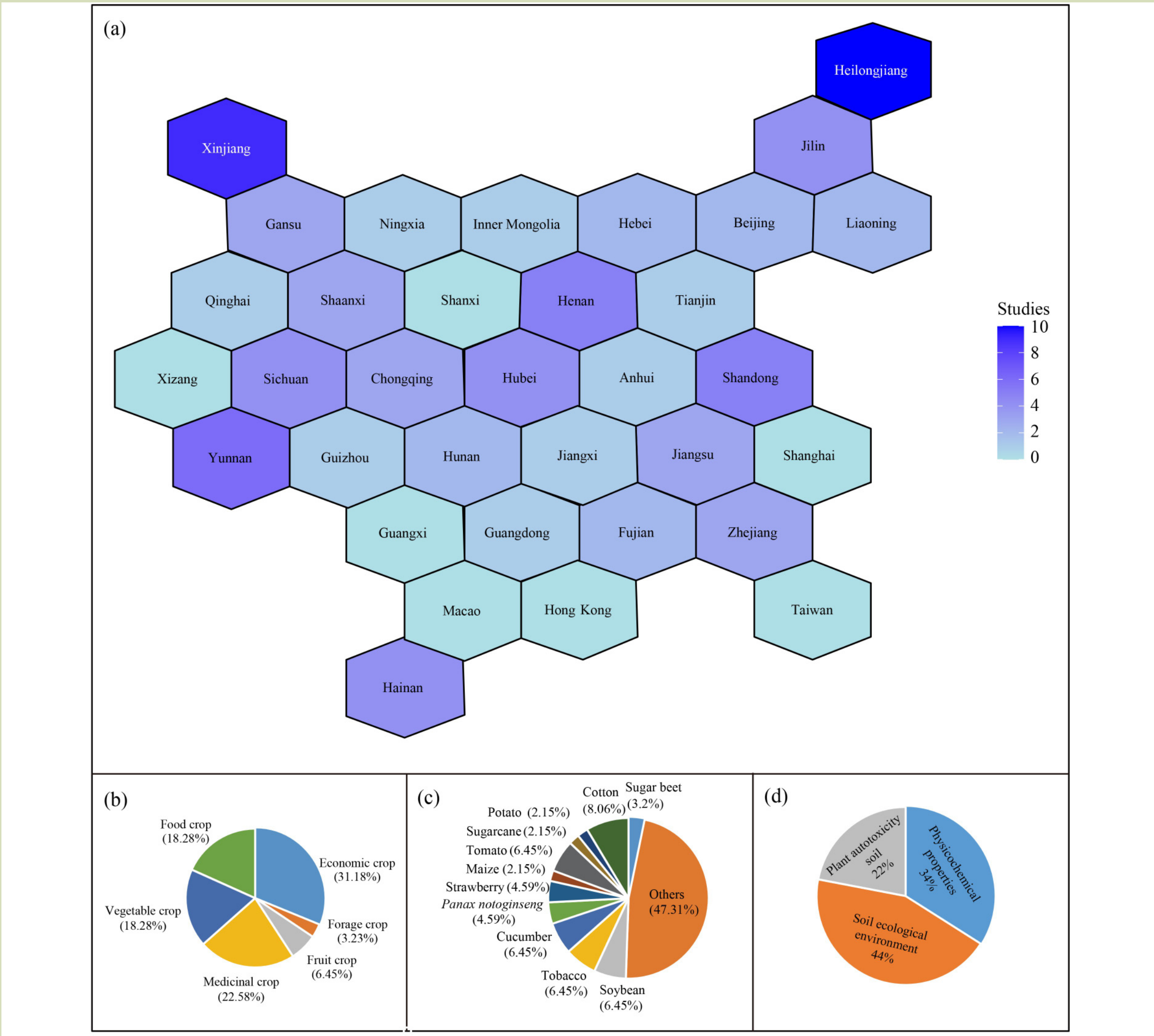


Fig. 2 Distribution of the database on different crops. (a) National distribution of study sites included in the meta-analysis; (b) proportions of crop types in the continuous cropping database; (c) proportions of various crops in the continuous cropping database; (d) proportions of different causes of continuous cropping obstacles.

revealed that continuous cropping significantly increased total nitrogen in the soil by 24% and significantly increased available nitrogen, phosphorus and potassium by 32%, 64%, and 37%, respectively (Fig. 3(a)). However, this imbalanced nutrient enrichment does not necessarily benefit the soil and plants. According to stoichiometry theory, a balanced ratio of essential nutrients is crucial for optimal plant growth and soil health. Excess nutrient accumulation in soil can lead to an imbalance in the stoichiometric ratio of nutrients, compromising their availability and utilization by plants. This imbalance can result in nutrient runoff and leaching, degrading soil quality and negatively impacting long-term crop productivity[32]. In addition, different plants have different nutrient requirements during the growth process. The selective absorption of soil nutrients, particularly trace elements, according to the physiologic needs of the plant during growth can also cause nutrient imbalance in soils, leading to various physiologic and functional disorders in crops that result in low yield and poor quality[33]. Also, improper water and fertilizer management during continuous cropping increases the base ion concentration in the soil, also known as electrical conductivity[34]. The analysis revealed that continuous cropping can increase electrical conductivity by 120% (Fig. 3(a)), which increases the risk for secondary soil

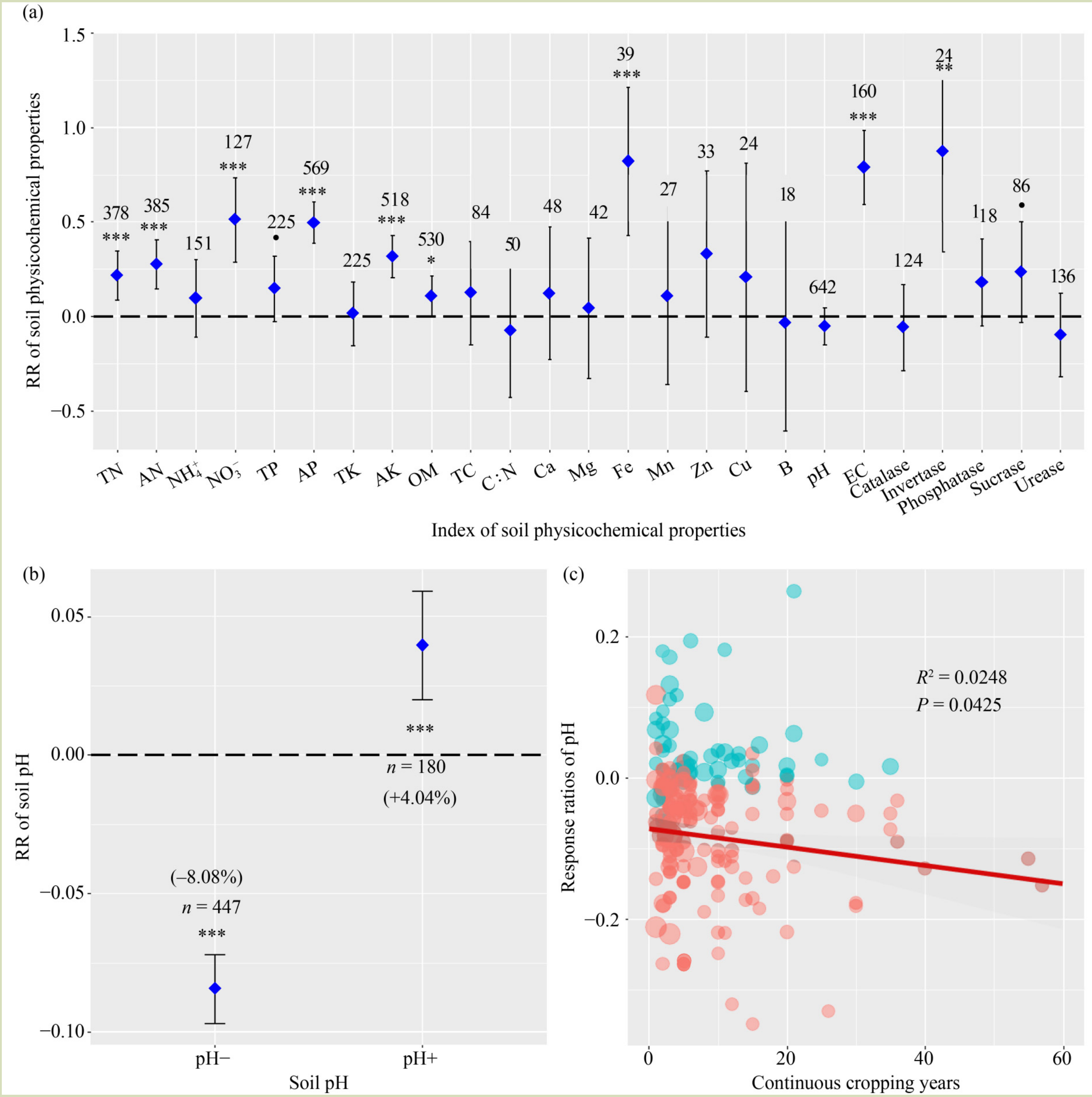


Fig. 3 Effects of continuous cropping on the physicochemical properties of soils. (a) Response ratio (RR) of physicochemical properties; (b) RR of acidification or alkalization; (c) meta-regression analysis of acidification degree in different continuous cropping years. TN, total nitrogen; AN, available nitrogen; NH_4^+, ammonia nitrogen; NO_3^-, nitrate nitrogen; TP, total phosphorus; AP, available phosphorus; TK, total potassium; AK, available potassium; OM, organic matter; TC, total carbon; C:N, carbon-to-nitrogen ratio; EC, cation exchange capacity; pH–, observations of acidified soil under continuous cropping; and pH+, observations on alkalized soil under continuous cropping. Red and green dots indicate studies on acidification and soil alkalinization caused by continuous cropping. The dashed line indicates mean RR = 0. Error bars represent 95% confidence intervals (CIs); numbers at the top and bottom of the CI are the numbers of observations. If a 95% CI did not overlap zero, the effect of continuous cropping on the variable was considered significant at various levels (•P < 0.1; *P < 0.05; **P < 0.001; and ***P < 0.0001).

salinization hazards that lead to crop yield reduction. Therefore, it is essential to consider the stoichiometric balance of nutrients in soil management practices to ensure sustainable agriculture and minimize the adverse effects of continuous cropping.

4.2 Plant autotoxicity

Autotoxicity, or self-toxicity, is a biological process where a species hinders the growth or reproduction of other members of its species by releasing certain chemicals into the environment[35]. Autotoxic substances have been found in many crops (Table 1). Notably, this effect harms crops directly while also facilitating the proliferation of pathogens, ultimately leading to poor crop growth, disease and death[53]. Studies have shown that phenolic acids such as *p*-hydroxybenzoic acid, vanillic acid and coumaric acid in peanut root exudates accumulate in soil with the extension of continuous cropping duration and exhibit inhibitory effects on peanut growth[54]. However, other studies have reached different conclusions, suggesting that phenolic acid compounds in peanut root exudates do not directly inhibit peanut growth but primarily disrupt the structure of soil microbial communities, leading to the proliferation of pathogenic bacteria in the soil and ultimately inhibiting peanut growth[41]. In addition to peanuts, medicinal herbs and leafy vegetable crops are also prone to allelopathic autotoxicity. In medicinal plants, after 3 years of consecutive cultivation, the rhizosphere soil of *Pseudostellaria heterophylla* has accumulated organic acids such as tartaric acid and succinic acid, and *P. notoginseng* has phenolic compounds. These autotoxic substances severely damage the microbial community, resulting in significant yield reduction or even complete crop failure[48,49]. In vegetable crops, continuous cropping of eggplant for 3 years resulted in cinnamic acid and vanillin secretion in root exudates, which inhibited the growth of seedlings and promoted the proliferation of a Fusarium wilt pathogen[55]. By comparison, continuous cropping of tomatoes for 7 years led to the accumulation of fatty acids in the rhizosphere soil, which inhibited seedling growth[44], and continuous cropping of cowpeas for 8 years resulted in the accumulation of organic acids such as benzoic acid in the rhizosphere, which inhibited the growth of seedlings[45]. The above studies have discovered different autotoxic substances related to continuous cropping and explored their harm to plants. The mechanism of plant allelopathy and autotoxicity in soil is much more complex than we imagined. Interspecific and intraspecific interactions among plants can be identified through chemical communication through released secondary substances, initiating corresponding growth and defense strategies, and producing corresponding allelopathic substances. Previous studies have revealed a density-dependent increase in DIMBOA concentration in wheat roots when co-

Table 1 Allelochemicals of different plants and their harmful effects on plants

Crop types	Crops	Allelochemicals and performance	Sources
Food crops	Barley	Barley root exudates inhibit root development in barley seedlings and weeds	[36]
	Rice	Some specialized metabolites found in rice straw have been proposed to be autotoxic: phenolic acids (e.g., ferulic acid (FA), *o*-hydroxy phenylacetic acid and *p*-coumaric acid), flavonoids, and terpenoids	[37]
	Potato	Water extracts from different organs of the potato exhibited an apparent inhibitory effect on the growth of the potato, and the extracts from the stem and leaves had a significant inhibitory effect on the height of the potato; the root extracts significantly inhibited the number of branches and stem diameter	[38]
	Wheat	DIMBOA is a specific allelopathic substance of wheat and other grass plants and plays a vital role in antibacterial, insect-resistant, and weed suppression	[39,40]
Economic crops	Peanut	Continuous cropping for 5 years; accumulation of phenolic acids in peanut rhizosphere; destruction of soil microbial community. Continuous cropping for four years; substances in peanut root exudates (e.g., myristic acid, palmitic acid, stearic acid, *p*-hydroxybenzoic acid, vanillic acid and coumaric acid) inhibited peanut growth	[41,42]
	Tobacco	*β*-cembrenediol, di-n-hexyl phthalate, and *bis*(2-propylheptyl) phthalate showed observable autotoxic activities on tobacco	[43]
Vegetable crops	Tomato	Continuous cropping for 7 years; accumulation of root exudate fatty acids in soil; tomato growth inhibition	[44]
	Cowpea	Continuous cropping for 8 years; accumulation of organic acids (e.g., cinnamic and phenylacetic acid) in soil inhibited cowpea growth	[45]
Fruit crops	Strawberry	Continuous cropping for 12 years; accumulation of phenolic acids such as *p*-hydroxybenzoic acid in soil	[46]
	Melon	The content of chlorophyll and carotenoid, photosynthetic rate, stomatal conductance, water-use efficiency, and transpiration rate decreased significantly in melon seedlings under autotoxicity	[47]
Medicinal crops	*Pseudostellaria heterophylla*	Continuous cropping for 3 years; accumulation of soil tartaric acid, succinic acid, and other organic acids; imbalance of soil microbial community	[48]
	Panax notoginseng	Continuous cropping for 3 years; accumulation of soil phenolic acids; imbalance of microbial community	[49]
Forage crops	Alfalfa	Root exudates and plant extracts negatively affect several traits related to germination and plant growth in the model legume *Medicargo truncatula*. Autotoxicity caused different oxidative stress strategies for the two alfalfa cultivars	[50,51]
	Forage rape	The residues of cultivated rape leave adverse effects on future crops; the observed effects are a reduction in plant dry weight, height, number of tillers per plant, and grain yield	[52]

cultivated with multiple weed species[56,57]. Kong et al.[39] found that (−)-loliolide and jasmonic acid are present in root exudates from diverse species and can trigger wheat allelochemical DIMBOA production. DIMBOA is a specific allelopathic substance of wheat and other grass plants and are important for antibacterial, insect-resistant and weed suppression[40]. Thus, the production of plant allelopathic substances involves a variety of complex signal exchanges within and between plant species. Starting from the ecological mechanism of allelopathy, exploring more allelopathic substances may be significant in alleviating plant autotoxicity.

4.3 Variations in the soil microbial food web

Continuous cropping can simplify the soil microbial food web and reduce its stability, reduce the diversity of nematodes and microorganisms in the soil, and increase the abundance of soilborne pathogens and phytophagous nematodes[7]. A meta-analysis showed that continuous cropping significantly reduces bacterial and fungal diversity in rhizosphere soils and significantly alters microbial community structure but has only a minor effect on beta diversity (Fig. 4(c)). A reduction in soil biodiversity can reduce niche competition between soilborne pathogens and other microorganisms in the non-parasitic. The destruction of soil microbial community structure disturbs microecological functions, creating suitable conditions for the outbreak of soilborne pathogens. Notably, diseases caused by soilborne pathogens are the most direct, primary manifestation of CCOs, with more than 70% of the damage caused by CCOs resulting from soilborne pathogens[58]. Data integration analysis showed that CCOs increased the plant disease index by an average of 395% (Fig. 5(a)). The most commonly reported soilborne pathogens caused by continuous cropping are soft rot, root rot, fusarium wilt, nematodes and ear rot diseases, which increase the plant disease index by an average of 35%, 30%, 22%, 20% and 15% (Fig. 5(c)).

The above studies enhance understanding of soil biological factors in continuous cropping. However, most current studies on biological factors of continuous cropping only focus on a single community of bacteria or fungi, and few studies focus on the interaction between nematodes, protozoa and multiple biological communities. According to data obtained from the Web of Science database, studies related to CCOs and biological communities showed that bacteria, fungi, nematodes and protozoa accounted for 50%, 46%, 3.7%, and 0.7%, respectively (Fig. 4(a)). There are 380 articles on single community research. By comparison, only five articles focus on the interaction of three or more communities (Fig. 4(b)). Studying the multitrophic interactions of soil microbial ecosystems from the perspective of soil food webs is significant to understanding of soil health. Soil degradation caused by continuous cropping will ultimately promote the abundance of pathogens and reduce the abundance of beneficial organisms by changing the soil microbial food web structure[2]. Although the study of CCOs from the perspective of soil food webs has not received much attention at present, it is believed that with the maturity of sequencing technology and the development of multiomics analysis technology in the future, analyzing CCOs from the perspective of soil food webs will become a research hotspot.

5 Incidence patterns of soilborne pathogens in continuous cropping soils

There are three main incidence patterns of disease caused by soilborne pathogens in continuous cropping (Table 2). Firstly, persistent severe, characterized by continuous serious plant disease during the entire continuous cropping process, resulting in severe crop yield reduction or even crop failure. For example, watermelon production will decrease by 25% after 21 consecutive years, and cucumber production will reduce by 50% after 20 consecutive years[59,60]. The main reason for this phenomenon is soil degradation and changes in the soil ecological environment caused by continuous cropping[2]. Secondly, reduced in later stages, manifestation is that diseases caused by soilborne pathogens are serious in the early stage of continuous cropping, pathogen-suppressive soil is formed in the later stage of continuous cropping, and plant diseases are reduced. Some researchers have proposed that soil exhibits self-healing properties against soilborne pathogens during continuous cropping. In the late stage of continuous cropping, plants recruit beneficial microorganisms to facilitate their resistance to soilborne pathogens, thereby triggering soil-specific immunity and forming a disease-suppressing soil[9]. For example, studies on soybean cyst nematodes have shown that the disease is severe within the first 5 years of continuous cropping but is gradually alleviated after that, accompanied by an enrichment of beneficial soil microorganisms, such as *Pseudomonas*; some studies that have focused on wheat take-all disease have demonstrated similar disease patterns after continuous cropping[12,75]. To verify this hypothesis further, we conducted a meta-analysis on the yield effects of crops under different continuous cropping years. The impact of continuous cropping on crop yield varies across studies. In most studies, it reduced crop yields. However, a few studies have found that continuous cropping can promote the formation of disease-suppressive soils, increasing crop yield in the later stages (Fig. S2). The yield-reduction effect of continuous cropping differs

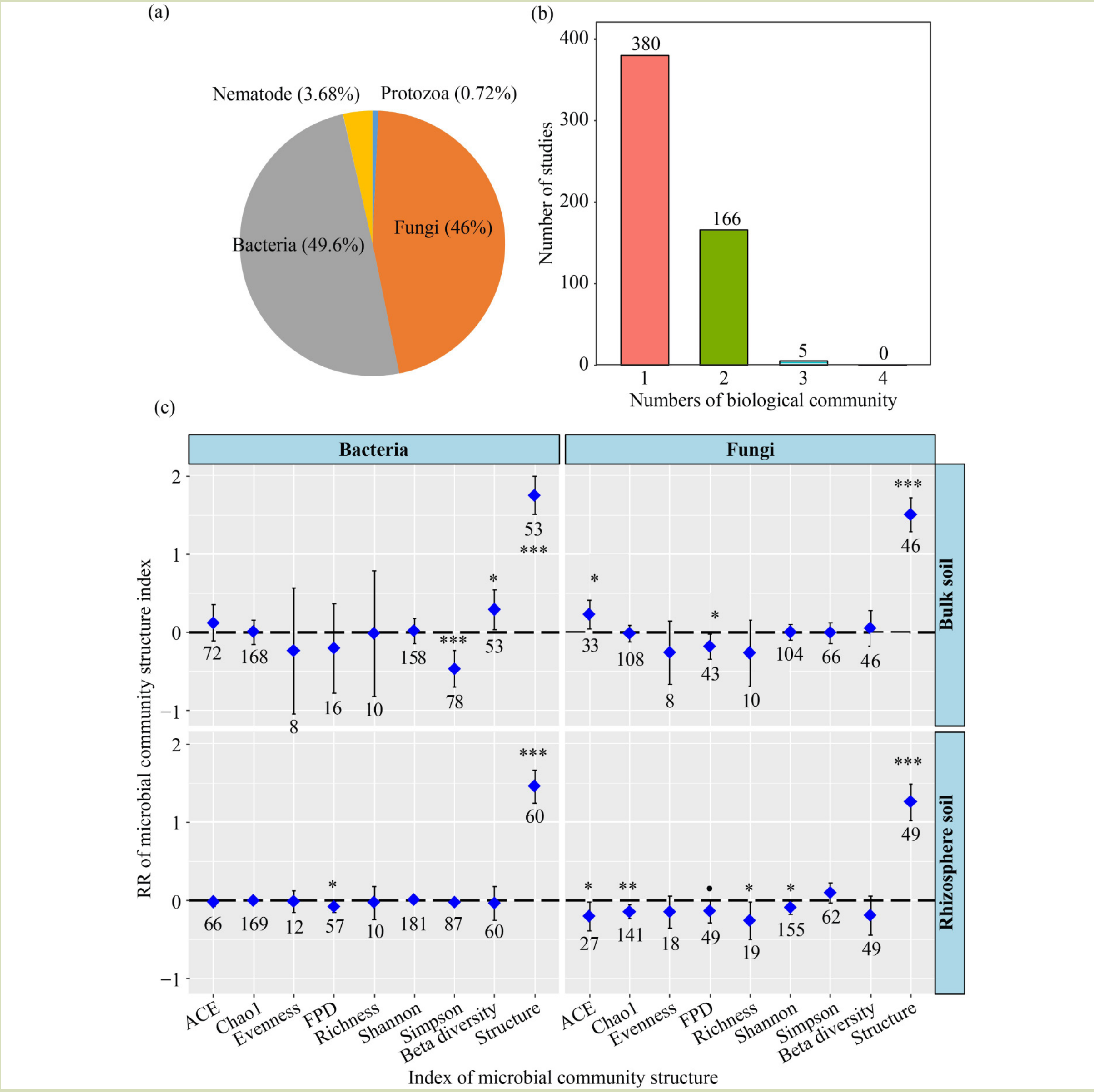


Fig. 4 Current status of research on the causes of continuous cropping obstacles. (a)The proportion of research on different biological communities in continuous cropping obstacles; (b) the number of studies on different numbers of biological communities (1 means studying only one community, 2 means studying the interaction of 2 communities, 3 means studying the interaction of 3 communities, and so forth); (c) microbial diversity index and community structure of bacteria and fungi in bulk soil and rhizosphere soil under continuous cropping. The dashed line indicates mean RR = 0. Error bars represent 95% CIs; numbers at the top and bottom of the CIs are the numbers of observations. If a 95% CI did not overlap zero, the effect of continuous cropping on the variable was considered significant at various levels (• $P < 0.1$; *$P < 0.05$; **$P < 0.001$; and ***$P < 0.0001$).

among crops. The yield of most crops will decrease with the increase of continuous cropping years. However, soybean yield does not change significantly with the rise of continuous cropping years. Some studies even found that continuous soybean cropping is conducive to forming pathogen-suppressive soil[10]. *Achyranthes bidentata* is a crop that tolerates continuous cropping, and continuous cropping is beneficial for increasing its yield (Fig. 5(b)). The analysis revealed that the yield-reduction effect caused by continuous cropping decreased with cropping duration, although this effect was insignificant (P = 0.058) (Fig. 6). We conclude that there may be a self-healing process in the soil in response to

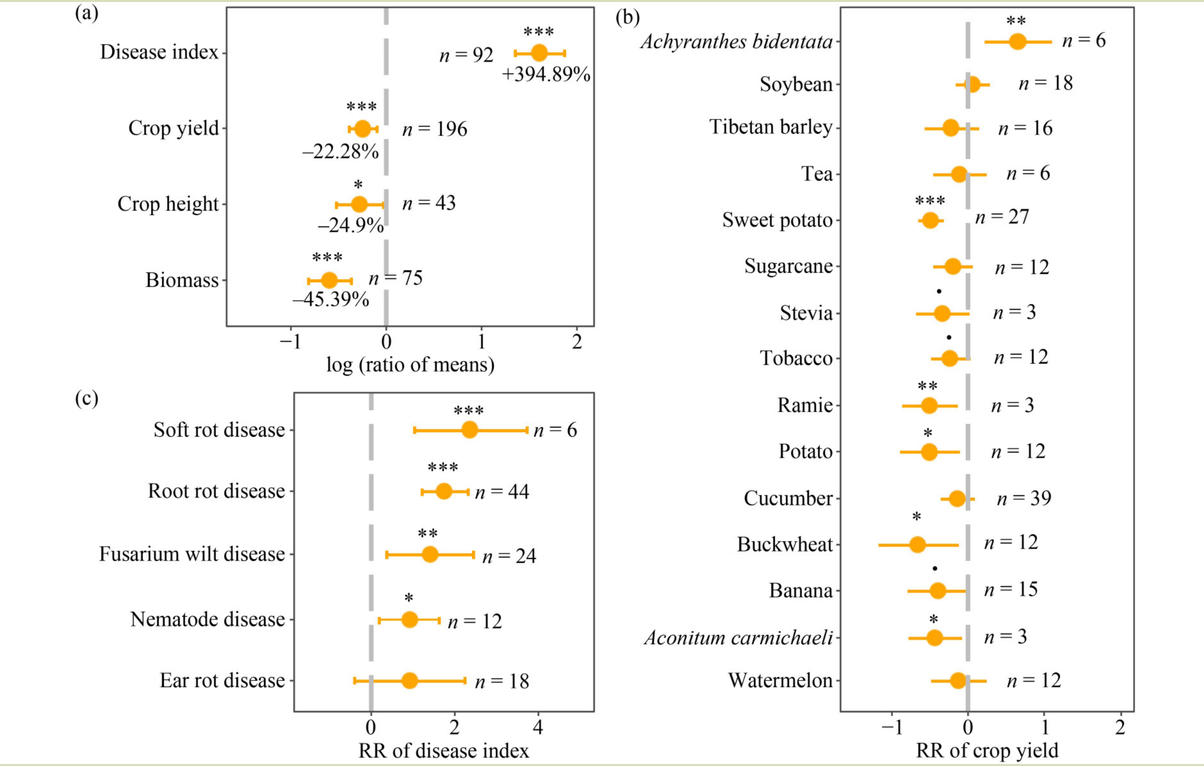


Fig. 5 Effects of continuous cropping on crop growth and disease index. (a) Response ratio (RR) of crop growth-related indicators; (b) RR of crop yield; (c) RR of the disease index for different soilborne pathogens. The dashed line indicates mean RR = 0. Error bars represent 95% CIs; numbers close to the CI are the numbers of observations. If a 95% CI did not overlap zero, the effect of continuous cropping on the variable was considered significant at various levels (•$P < 0.1$; *$P < 0.05$; **$P < 0.001$; and ***$P < 0.0001$).

continuous cropping stress. Finally, continuous fluctuation, which is characterized by a cycle of alternating severe disease periods and milder disease periods during continuous cropping. The reason for this phenomenon may be the result of the coevolution of plants and pathogens. Jones and Dangle proposed the zigzag model to explain the co-evolution of plant immunity and pathogen infection in detail at the molecular level[76].

6 Comprehensive mitigation measures for CCOs

The regulation of soil health can be achieved through various measures including physical, chemical and biological interventions to manage the rhizosphere ecosystem comprehensively. This process involves regulating the ecology of soil and crop growth processes and interactions among soil organisms to maintain soil health and provide adequate protection effectively[77]. Soil organisms do not exist in isolation but form a complex network interacting through symbiosis, competition, predation and other mechanisms that collectively contribute to ecological regulation[7]. Previous studies on CCOs have largely overlooked the role of biological regulation and the regulatory effect of the microbial food web on nutrient cycling and energy flow. There has been an excessive focus on fertility indicators and an overreliance on management practices that depend heavily on excessive irrigation, excessive fertilizer use and chemical inputs. This approach is taken at the expense of the environment and sustainability of soils and severely impacts the safety and quality of agricultural products. It also significantly hinders sustainable agricultural development and efficient resource utilization. Therefore, based on the multi-factor induction mechanism of CCOs, breakthroughs in the reduction of CCOs should be made in the following aspects in the future.

6.1 Scientific and accurate management of fertilizer

During continuous cropping, farmers often rely on excessive mineral fertilizer application as the primary method to improve soil fertility and increase crop yield while neglecting the use of organic fertilizers. This practice increases production

Table 2 Incidence patterns of disease caused by soilborne pathogens in continuous cropping soils

Incidence pattern	Crop	Disease	Continuous cropping period and performance	Source
Persistent severe	Watermelon	Unknown	21 years of continuous cropping changes soil physical and chemical properties and microbial community composition, thereby reducing watermelon yields	[59]
	Cucumber	Unknown	During 20 years of continuous cropping, soil degradation caused cucumber yield and quality to continue to decrease	[60]
	Vanilla	Stem rot	During the 21 years of continuous cropping, stem rot became more serious yearly. Soil weakness and vanilla stem wilt disease after long-term continuous cropping can be attributed to the alteration of the soil microbial community membership and structure, i.e., the reduction of the beneficial microbes and the accumulation of the fungal pathogen	[61]
	Maize	Blight Ear rot	The highest disease incidence of seedling blight and ear rot was 8.2% in 20 years of continuous cropping and 13% in 30 years, respectively	[62]
	Sugarcane	Unknown	Continuous cropping for 30 years changes microbial communities by changing soil physical and chemical properties, thereby causing crop yield reductions	[63]
	American ginseng *Panax notoginseng* *Aconitum carmichaeli*	Root rot	Severe diseases occur in short-term continuous cropping of such medicinal crops, but the impact of long-term continuous cropping on diseases is unknown	[64–66]
	Soybean	Root rot	During 20 years of continuous cropping, harmful microorganisms decreased, beneficial microorganisms increased, and diseases were reduced	[67]
Reduced in later stages	Wheat	Take-all	Wheat take-all disease is reduced in the late stage of continuous cropping. Pseudomonas fluorescens that produce the antibiotic 2,4-diacetylphloroglucinol are the major determinant of the suppressiveness of take-all	[68–70]
	Soybean	Unknown	During 13 years of continuous cropping, the abundance of archaea increased, and the abundance of harmful microorganisms decreased. Archaeal communities perform an important role in maintaining microbial stability under long-term continuous cropping systems	[10]
	Soybean	Cyst nematode	Continuous cropping reduces the abundance of soil cyst nematodes by increasing the abundance of beneficial soil microorganisms	[12]
	Tobacco	Unknown	The continuous cropping obstacles were severe in the first 5 years; however, after 15 years, the yield gradually recovered, and the soilborne pathogens were significantly inhibited	[71]
	Wheat	Bare patch	In the 5th to 7th year of continuous cropping, the area of bare patches reaches a peak, starts to decrease in the 8th year, and approaches 0 in the 11th year	[72]
Continuous fluctuation	Banana	Wilt	The disease occurred seriously after 6 and 11 years of continuous cropping but was milder after 1 and 10 years	[73]
	Cotton	Unknown	Cropping is the leading cause of changes in the structure of the bacteria community; however, the new structure formed under the continued duress of long-term cotton cultivation, and the associated farming methods gradually stabilized after 10 years of repeated fluctuations	[74]

costs and leads to a series of problems, including soil compaction, acidification and salinization, as well as groundwater pollution and excessive nitrate levels[78]. In comparison, organic fertilizers provide a more balanced supply of nutrients and enhance soil water and nutrient retention capacity. Long-term application of organic fertilizers promotes the formation of soil aggregates, improves the physical and chemical properties of soils, mitigates issues caused by excessive mineral fertilizer use, and enhances disease suppression in soils[79]. In addition, organic fertilizers can regulate the structure of the microbial food web. Increasing the application of organic fertilizers improves the rate of bacterial degradation and affects the activity and function of nematodes at lower trophic levels in the food web. From the perspective of the nematode community structure and function in the soil, appropriate increases in organic fertilizer application can promote nutrient cycling and energy flow within the soil microbial food web[80]. Therefore, reducing the use of mineral fertilizers and partially substituting these with organic fertilizers are important measures for mitigating CCOs. Also, different crops have different nutrient requirements at different growth stages. It is necessary to scientifically tailor fertilizer applications based on soil properties, fertilizer characteristics and crop traits. This is essential to improve overall soil nutrient utilization efficiency and alleviate problems associated with improper fertilizer management during continuous cropping.

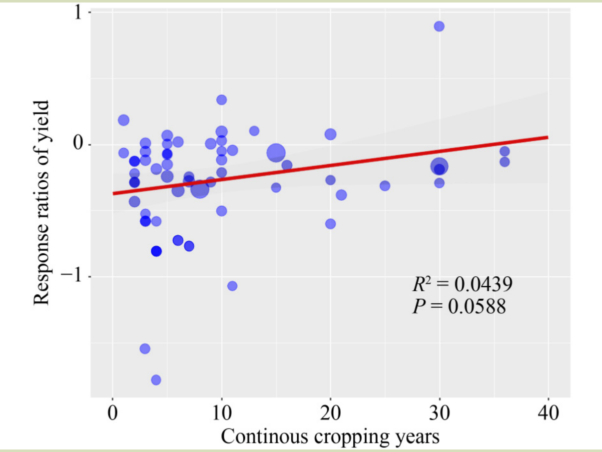


Fig. 6 Effects of continuous cropping years on crop yield reduction. Blue dots indicate the effect value corresponding to each observation point; point size is proportional to its weight. The red line represents the fitting curve, and the shading represents the 95% CI.

6.2 Optimizing cropping patterns

Optimizing the cropping patterns and breaking the cycle of monoculture is the most direct approach to overcoming CCOs. A positive correlation between biodiversity and ecosystem functioning has long been established, and evidence suggests that plant community diversity influences soil microbial diversity and functions, thereby promoting functions necessary for sustainable agriculture[81]. Crop rotation and intercropping are commonly applied strategies for optimizing cropping patterns. Proper crop rotation can effectively regulate imbalances in soil microbial communities caused by continuous cropping, restore soil ecosystem services, and mitigate biological obstacles associated with continuous cropping. For example, banana-pineapple rotation significantly reduces the incidence of banana soilborne wilt and pineapple residues can induce an increased abundance of antagonistic fungi such as *Trichoderma* and *Fusarium*, promoting the formation of suppressive soils[82]. Rotation with leguminous crops such as faba beans can improve the physicochemical properties of soils, enhance enzyme activity and increase crop yield[83]. Intercropping can enhance the plant root system, nutrient availability and nutrient uptake efficiency promoting microbial activity. In a maize-peanut intercropping system, peanut rhizobia contributes to nitrogen fixation, improving the available nitrogen nutrition for maize plants; the maize, in turn, releases exudates that increase available iron that benefits peanuts[84,85]. Intercropping cassava and leguminous crops increases nutrient use efficiency and soil microbial diversity and significantly reduces the incidence of cassava root rot[86]. Studies on peanut-cassava intercropping have shown that cyanide produced by cassava can induce ethylene signaling in intercropped peanuts, reshaping the rhizosphere microbial community, which in turn accelerates organic nitrogen and phosphorus mineralization, thereby improving nitrogen and phosphorus nutrient utilization and peanut yield[87]. Thus, optimizing cropping patterns is a sustainable and practical approach to addressing the challenges of continuous cropping.

6.3 Conservation tillage

Conservation tillage refers to agricultural practices aimed at minimizing destructive mechanical operations while ensuring the sustainable use of agricultural, water, and soil resources[88]. Techniques such as reduced tillage and no-till farming are considered forms of conservation tillage. Applying traditional tillage methods during continuous cropping involves frequent soil disturbance that can lead to soil compaction, nutrient and water loss, soil aggregate disruption, and reductions in organic matter content. Conservation tillage reduces soil disturbance by minimizing the number of large-scale mechanical field operations, thereby mitigating structural damage and moisture evaporation from the surface. This improves soil aggregates and organic matter content, reducing production costs and enhancing crop yields. A meta-analysis on north-eastern China indicates that conservation tillage can increase yields by about 0.8% compared to standard ridging and about 13.1% compared to deep tillage while also increasing organic carbon content by 17.4% to 43.9%[89]. Conservation tillage can also change the soil microbial food web structure and promote soil health by increasing soil nematode abundance and maturity index, soil microbial biomass and diversity[90]. Increasing attention has recently been focused on implementing appropriate conservation tillage practices.

6.4 Biological control

The primary mechanism of crop yield reduction caused by CCOs is soilborne pathogens caused by an imbalance of the soil microbial food web; therefore, improving the health level of continuous cropping soil from the perspective of regulating soil microbial food web stability would help achieve sustainable crop yield increases. Disease-suppressive soils harbor many beneficial microorganisms in the natural environment. In the form of biological control for continuous cropping soil, beneficial microorganisms in various complex environments, including disease-suppressing soil, are screened in a targeted manner, cultured in a laboratory, and then returned to disease-susceptible soils in the form of bacterial agents or bio-organic fertilizers; this helps produce a healthy and stable microbial food web structure[91]. Beneficial microorganisms in the soil effectively promote organic phosphorus mineralization, enhance the bioavailability of soil nutrients and inhibit soilborne pathogens through mechanisms such as inducing plant resistance, antagonizing pathogens and competing for ecological niches[92–94]. Commonly applied exogenous microbial agents include species of *Bacillus*, *Pseudomonas*, *Penicillium*, *Streptomyces*, *Trichoderma* and arbuscular mycorrhizal fungi. *Bacillus* has been widely applied in controlling soilborne pathogens such as wilting pathogen, soft rot bacteria and root-knot nematodes. For example, *Bacillus amyloliquefaciens* has been shown to synergistically suppress banana wilt disease in conjunction with *Pseudomonas*[95–97], and arbuscular mycorrhizal fungi can activate soil phosphorus and promote its availability[98]. These microorganisms can also induce plant resistance, indirectly helping plants to suppress diseases[99].

Another biological control method is to identify functional substances of plant origin or microbial origin in nature and apply them in the field. In nature, there are host and non-host plant of various soilborne pathogens, and for some host crops there are resistant and susceptible cultivars. Therefore, developing multiple experimental methods to explore functional substances in the root exudates of non-host plants and resistant cultivars will benefit the eco-friendly and efficient control of soilborne pathogens. Root-knot nematode is a common soilborne organism found in continuous vegetable cultivation in China. A comparison of the differences in root exudates between tomato, a root-knot nematode host plant, and *Garland chrysanthemum* and *Ricinus communis*, which are non-host plants, led to the identification of lauric acid as a root exudate from *G. chrysanthemum* and palmitic acid and linoleic acid as root exudates from *R. communis*. These three substances exhibited inhibitory effects on the hatching and mortality of second-stage juveniles of the *Meloidogyne incognita*. They interfered with nematode migratory behavior by regulating the expression of the *Mi-flp-18* gene[100]. In another study, functional substances for controlling the southern root-knot nematode were identified and screened from fermented chicken manure and waste liquid from cassava alcohol production, leading to the discovery that methyl palmitate, methyl stearate, and triethyl phosphate, which cause mortality in second-stage nematode juveniles, inhibited nematode egg hatching and repelled second-stage juveniles. Significantly, these functional substances did not impact the reproduction of beneficial soil nematodes such as the free-living *Caenorhabditis elegans*[101,102]. These studies provide necessary theoretical and technical foundations for developing environmentally friendly nematode control agents and functional green, intelligent fertilizers.

7 Conclusions

In recent years, soil CCOs have become an agricultural research hotspot worldwide, and significant progress has been made in researching this issue. CCOs are the outward manifestations of the comprehensive interactions among plants, soil, microorganisms and the environment. Continuous cropping can lead to the accumulation of phenolic acids, sustained soil acidification, increased soilborne pathogens, and reduced beneficial microorganisms, ultimately resulting in an imbalance of the entire soil microbial ecosystem and significant crop yield reduction. Pathogen-suppressive soil has stable physical and chemical properties and can enrich beneficial soil microorganisms to contribute to the resistance of plants to soilborne pathogens (Fig. 7). Based on the rhizobiont theory[103], nutrient absorption occurs across multiple interfaces (soil-organisms-plants). Therefore, addressing CCOs requires their mitigation among these interfaces.

Widely-established cultivation practices depend heavily on excessive irrigation, intense fertilizer application and chemical pesticide usage. This approach has been taken at the cost of the health and sustainability of the soil environment, with significant impacts on the safety and quality of agricultural products. Therefore, fertilizers and pesticides must be applied scientifically and rationally, for example, by partially replacing mineral fertilizers with organic fertilizers and chemical agents with biocontrol agents.

Soil organisms are also crucial for soil health and represent the biological foundation for soil immunity and disease suppression. Nematodes and other microorganisms in the soil are critical components of the soil community, and their interactions are essential for various ecosystem functions, such as the decomposition and mineralization of organic matter and geochemical elemental cycling[104]. Therefore, more attention must be given to the role of biological indicators in assessing CCOs through measures such as proper fertilizer management, optimized cropping patterns and conservation tillage to regulate the structure of the soil microbial food web.

Finally, we emphasize that continuous cropping does not always worsen soil health; it can also improve soil conditions and form pathogen-suppressive soils. It is necessary to fully excavate the microbial resources in pathogen-suppressive soil

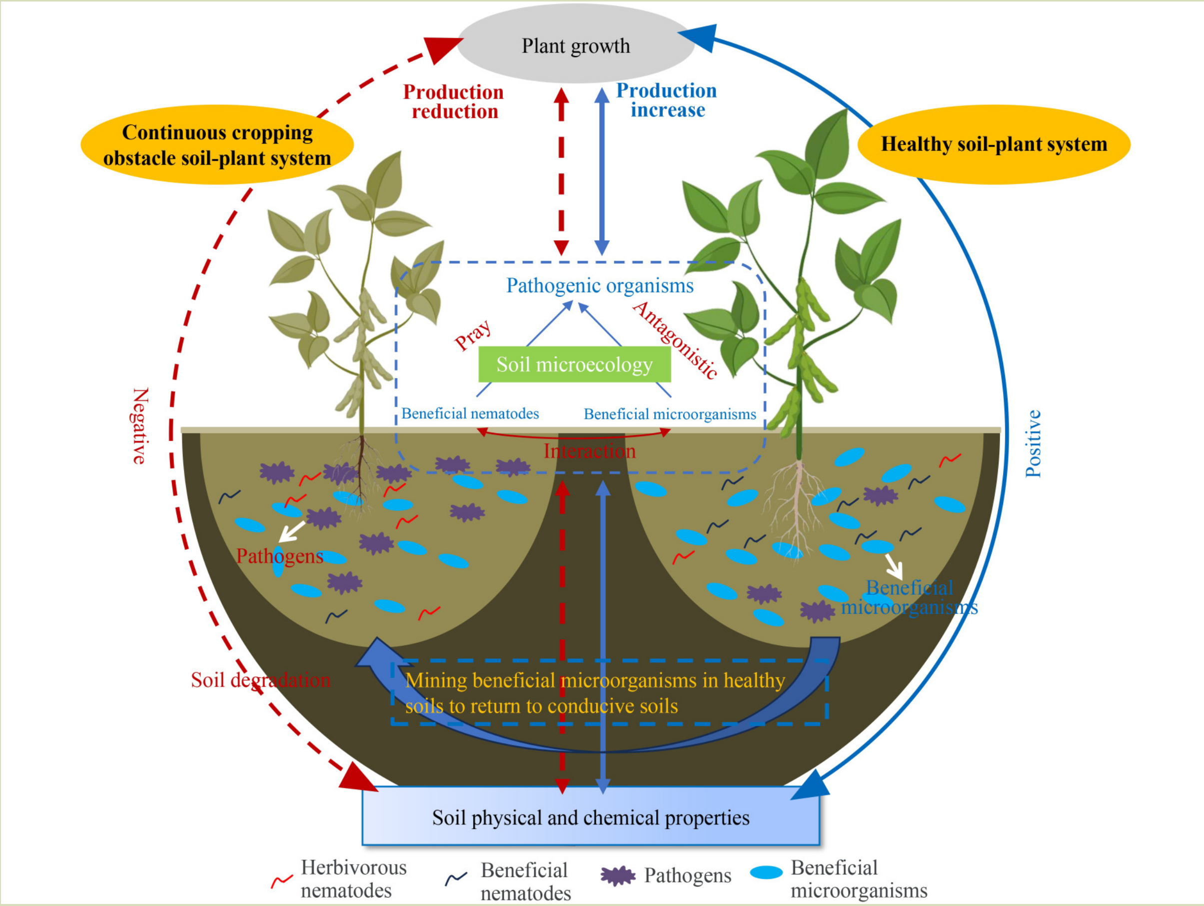


Fig. 7 Conceptual model of the effects and the regulation mechanisms of continuous cropping on plant growth, soil physical and chemical properties, and soil microbial communities and their interactions.

during the late stage of continuous cropping, cultivate and enrich these beneficial microorganisms, and return them to non-suppressive soil to regulate the microecological community. This practice will allow us to achieve stable crop yields, improve productivity, and promote sustainable agricultural development.

Supplementary materials

The online version of this article at https://doi.org/10.15302/J-FASE-2024543 contains supplementary materials (Figs. S1–S2).

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Compliance with ethics guidelines

Kunguang Wang, Qiaofang Lu, Zhechao Dou, Zhiguang Chi, Dongming Cui, Jing Ma, Guowei Wang, Jialing Kuang, Nanqi Wang, and Yuanmei Zuo declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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