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REVIEW

INTERCROPPING: FEED MORE PEOPLE AND BUILD MORE SUSTAINABLE AGROECOSYSTEMS

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KEYWORDS

agroecosystems, crop diversity, intercropping, interspecific interactions, sustainable agriculture

HIGHLIGHTS

- Intercropping is a useful practice when agricultural sustainability is emphasized.
- We integrate biodiversity-ecosystem functioning and intercropping.
- Intercropping optimizes ecosystem services such as stabilizing yield and reducing use of chemicals.
- Intercropping benefits are attributed partly to complementarity and selection effects.
- Application of ecological principles is key to sustainable agricultural development.

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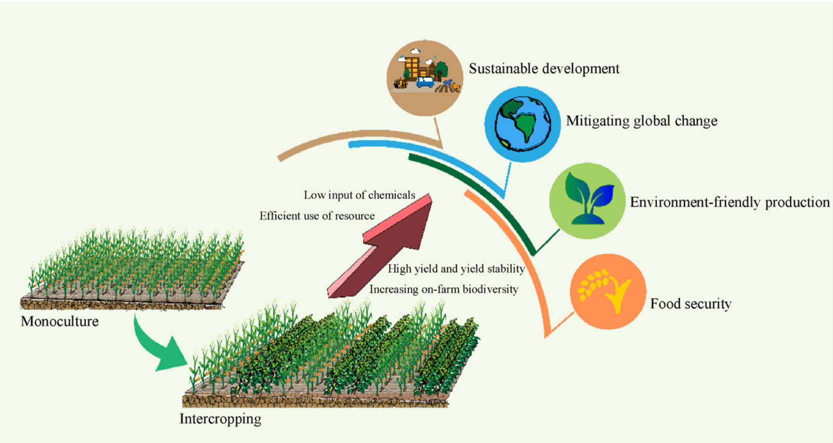
GRAPHICAL ABSTRACT



ABSTRACT

Intercropping is a traditional farming system that increases crop diversity to strengthen agroecosystem functions while decreasing chemical inputs and minimizing negative environmental effects of crop production. Intercropping is currently considerable interest because of its importance in sustainable agriculture. Here, we synthesize the factors that make intercropping a sustainable means of food production by integrating biodiversity of natural ecosystems and crop diversity. In addition to well-known yield increases, intercropping can also increase yield stability over the long term and increase systemic resistance to plant diseases, pests and other unfavorable factors (e.g., nutrient deficiencies). The efficient use of resources can save mineral fertilizer inputs, reduce environmental pollution risks and greenhouse gas emissions caused by agriculture, thus mitigating global climate change. Intercropping potentially increases above- and belowground biodiversity of various taxa at field scale, consequently it enhances ecosystem services. Complementarity and selection effects allow a better understanding the mechanisms behind enhanced ecosystem functioning. The development of mechanization is essential for large-scale application of intercropping. Agroecosystem multifunctionality and soil health should be priority topics in future research on intercropping.

1 CROP DIVERSIFICATION AS A POTENTIAL SOLUTION TO THE PROBLEMS OF INTENSIVE MONOCULTURES

1.1 Problems of intensive monocultures

Global food demand is an increasingly crucial challenge for humanity. Over the last 50 years, intensive agriculture has increased food production by the use of high-yielding crop cultivars, greater inputs of fertilizers, and water and pesticides[1], and has contributed greatly to feeding humanity. However, intensive agriculture often pursues the maximization of the productivity of monocultures and crop diversity in intensive agricultural systems is often reduced to one species which is usually genetically homogeneous[2]. Intensive agriculture incurs negative environmental impacts such as greenhouse gas emissions, soil erosion and degradation, and loss of biodiversity[3]. Soil acidification is a major feature in soils of intensive Chinese agricultural systems. Two nationwide surveys show that soil pH in China declined significantly from the 1980s to the 2000s[4]. Due to increasing application rates of synthetic nitrogen fertilizers, the rate of nitrous oxide emission in atmosphere has increased rapidly[5]. Simultaneously, the biodiversity of agroecosystems in Europe has been significantly negatively related to N inputs[6].

Decreasing farmland biodiversity in intensive agroecosystems is a major concern for food security and global climate change[7]. In contrast, multicropping systems increase on-farm biodiversity and have potential advantages in yield and yield stability, pest and disease control, and reducing fertilizer use, and therefore provide an efficient sustainable approach to ensure food security with minimal environmental costs[2].

1.2 Monoculture to crop diversification: one solution for modern agricultural problems

Species diversity is a major determinant of ecosystem productivity, stability, invasibility and nutrient dynamics[8]. Crop diversification in agroecosystems can be increased on a temporal scale via crop rotations and on a spatial scale via cover crops, crop mixtures, agroforestry and intercropping[2]. Crop rotation involves growing different crops in different seasons in the same field. Rotation of different crops reduces disease inoculum due to host absence and organic residues that can affect the pathogens or antagonistic organisms[9]. A cover crop is defined as any living ground cover that is planted with or after the main crop, and usually killed before the next crop is planted, and a cover crop is used primarily for erosion control, improving soil health, enhancing water availability, helping to control weeds, insects and diseases, and increasing biodiversity in a farming system[9]. Crop mixtures are two or more different crop species or different cultivars of the same crop species grown simultaneously in the same field in alternate rows or mixture with no distinct row arrangement[10]. Of the different kinds of crop diversification in agroecosystems, intercropping, which grows at least two crops simultaneously at the same field, has attracted considerable interest because of its great potential to increase biodiversity and use resources, when more attention is given to sustainable agriculture development[11].

1.3 Current types and distribution of intercropping all over the world: China and globally

Intercropping has a history of thousands of years in China and other parts of the world. Intercropping is an ancient farming system that is still widely practiced by smallholders not only in China, but also in India, Africa and Latin America (Table 1). In Latin America, 70%–90% of beans are grown with maize, potatoes and other crops, 98% of cowpeas (*Vigna unguiculata*) and 90% of beans are grown in intercropping in Africa and Colombia[29]. Intercropping provides benefits to smallholders in Africa through increased crop yields and income as well as increased resource use[29]. A meta-analysis indicates that intercropping increases crop yields by 23% and gross income by 172 USD·ha^{-1} in Africa on average[30]. Intercropping is practiced in almost every province in China, with the type of intercropping more diverse in the east than in the west and more diverse in the south than in the north[31]. About a third of the total arable land is used for multicropping, of which 33 Mha of arable land was used for intercropping in the 1990s in China[32]. A recent study indicates that intercropping was practiced on about 3% of the arable land in 68 villages across six Chinese provinces in 2014[32]. In Europe, there is currently less common use by farmers but scientists and agronomists have endeavored to use crop diversification to solve issues with intensive agriculture[33]. An intercropping system with legume cover crops demonstrates that legumes can increase soil cover and increase soil fertility in farmland[23]. Also, intercropping of forages such as peas (*Pisum sativum*) and barley (*Hordeum vulgare*) provides higher quality feed[24].

2 WHY INTERCROPPING IS SUSTAINABLE

In contrast to natural ecosystems, intensive agroecosystems have many unique characteristics such as decreased plant diversity,

Table 1 Distribution and land equivalent ratio (LER) of the main intercropping systems of selected countries

Continent	Country/Region	Intercropping system	LER	Reference
Africa	Ethiopia	Wheat (*Triticum aestivum*)-faba bean (*Vicia faba*)	1.03–1.17	[12]
	Malawi	Maize (*Zea mays*)-pigeon pea (*Cajanus cajan*)	–	[13]
	Nigeria	Rice (*Oryza sativa*)-cowpea	1.13–1.85	[14]
Asia	China	Maize-pea	1.18–1.47	[15]
		Wheat-maize	1.14–1.33	[16]
		Maize-soybean (*Glycine max*)	1.91–2.13	[17]
		Maize-faba bean	0.94–1.47	[18]
	India	Maize-soybean	1.1–1.6	[19]
		Rice-peanut (*Arachis hypogaea*)	1.66	[20]
	Iran	Sunflower *(Helianthus annus)*-soybean	0.82–1.28	[21]
Europe	England	Maize-faba bean	1.02–1.23	[22]
	France	Wheat-clover (*Trifolium*)	–	[23]
	Italy	Ryegrass (*Lolium perenne*)-clover	1.1–1.2	[24]
North America	Canada	Pea-barley (*Hordeum vulgare*)	1.13–1.31	[25]
		Pea-oat (*Avena sativa*)	1.13–1.29	[25]
	United States	Winter wheat-clover	–	[26]
Oceania	Australia	Wheat-chickpea (*Cicer arietinum*)	0.97–1.10	[27]
South America	Brazil	Cowpea (*Vigna unguiculata*)-beet (*Beta vulgaris*)	1.05–1.11	[28]

increased inputs of mineral fertilizers and pesticides, and monocultures of high-yielding cultivars[34]. Compared to intensive agriculture, intercropping can increase yield and yield stability, utilize resources efficiently, suppress pests and diseases, mitigate climate change, control soil pollution and increase on-farm biodiversity, which can contribute to the sustainable intensification of agriculture if the aim is to increase yields without compromising environmental integrity (Fig. 1)[1].

2.1 Increasing yield and stability of productivity

Numerous studies show that intercropping has yield advantages compared to monoculture (Fig. 1(a)). The land equivalent ratio (LER) is defined as the relative land area under monoculture that is required to produce the yields achieved in intercropping and is used to assess crop performance in intercropping relative to monoculture[35]. A meta-analysis has found that intercrops were more efficient in land use than monocultured crops, with 434 out of 552 calculated LERs >1[36]. In another meta-analysis including 126 studies that covered 41 countries, intercrops produced 38% more biomass (mean relative land output of 1.38) compared to monocultures[37].

In barley and faba bean mixed cropping in the Ethiopian highlands, increasing the percentage of faba bean from 13% to 63% increased faba bean grain yields from 12% to 48% but lowered barley grain yields from 93% to 73% of the corresponding monoculture yields. At the same time, mean values of LER ranged from 1.05 to 1.23 in different mixed proportions of barley and faba bean[38]. Maize-common bean (*Phaseolus vulgaris*) intercropping is widely practiced by smallholders in sub-Saharan Africa, and the LER of maize intercropped with two cultivars of common bean were 1.48 and 1.55[39]. The LERs show that plant growth resources were used on average 5%–10% more efficiently with N application and 20% more efficiently without N application in pea-barley intercropping[35]. Sorghum (*Sorghum bicolor*)-desmodium (*Desmodium intortum*) intercropping significantly increased grain yields by 63% compared to monocultures in East Africa[40]. In India, intercropping soybean and pigeon pea yields higher than monocultures, and the area-time equivalent ratio (ATER) was 1.27[41]. Compared to the weighted means of corresponding monocultures, the average total grain yields of rape (*Brassica campestris*)-maize, faba bean-maize, chickpea-maize and soybean-maize intercropping systems increased by 31%, 24%, 45%, and 39%, respectively, in northwest China[18].

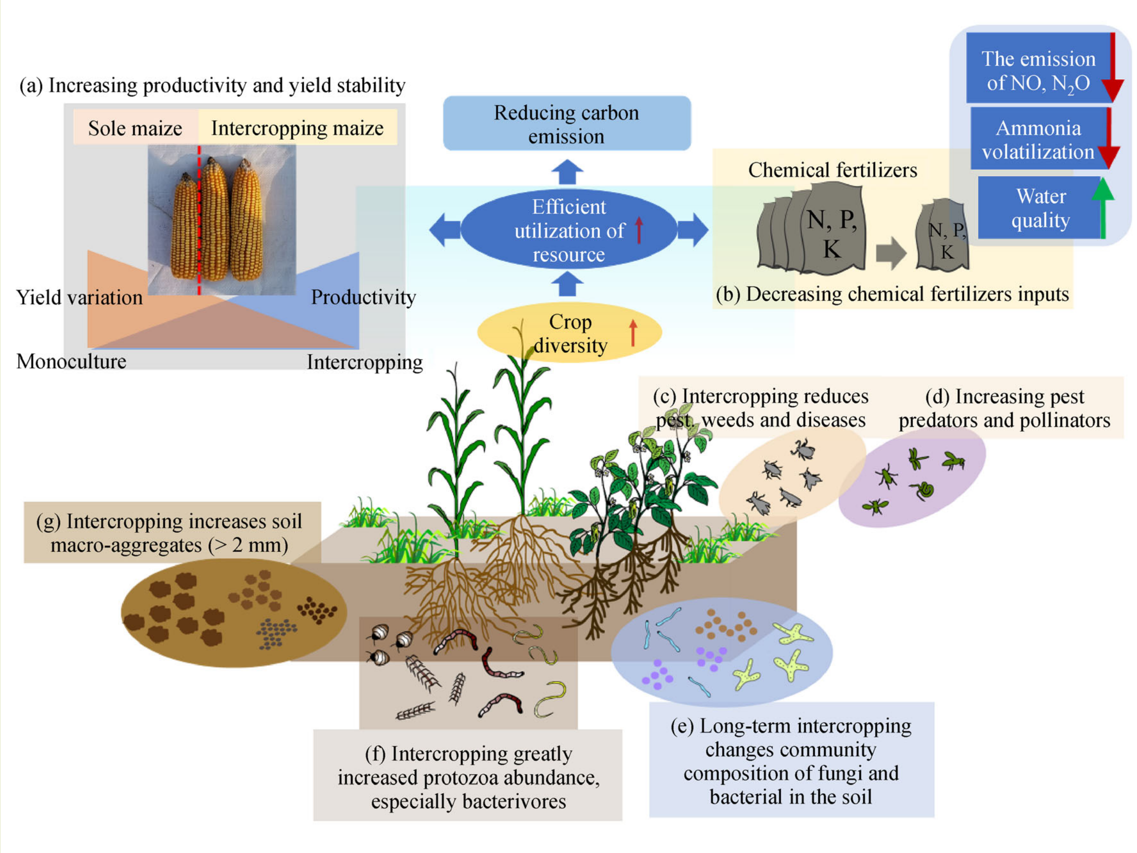


Fig. 1 Crop diversity and the coexistence of multiple species have been used as an example of improved agroecosystem functions. Compared to monocultures, intercropping increased the productivity and yield stability, reduced agrochemical inputs and thus the environmental costs (greenhouse gas emissions, water and soil pollution), and increasing insect diversity improved crop pollination and reduced plant diseases. Intercropping increases soil fertility in terms of chemical, biological and physical properties.

Intercropping saves the cultivated area while increasing productivity, offering a great opportunity for sustainable intensification of agriculture.

Temporal stability of productivity, an important indicator of agricultural sustainability, is often calculated as the mean biomass of a community or of each species divided by its temporal standard deviation[42]. Biodiversity increases the temporal stability of community biomass and decreases that of species biomass in a decade-long grassland experiment[42]. Compared to rice monoculture, a field survey demonstrated that a rice-fish co-culture system had similar rice yields and rice-yield stability but required 68% less pesticide and 24% less mineral fertilizer[43]. In experimental and participatory research with crop diversity (including rotation, semiperennial rotation, intercropping and semiperennial intercropping systems) in Africa, semiperennial rotation systems at half-fertilizer rates produced equivalent quantities of grain, on a more stable basis (yield stability increased from 13% to 22%) compared to monoculture. Crop diversification with legumes can enhance environmental and food security in Africa[13]. Through meta-analysis of data from 94 sorghum-pigeon pea intercropping experiments, the yield stability of the intercropping system was shown to be higher than in monocultures, especially under stress situations, estimating the probability of cropping systems failing to given ‘disaster’ levels of monetary returns, monocultured pigeon pea would fail approximately one year in five, monocultured sorghum one year in eight, but intercropping only once in 36 years under a particular disaster level[44]. The meta-analysis compared yield stability in intercropping with the respective monocultures from 33 published papers and found that cereal-grain legume intercropping (CV = 22%) significantly increased yield stability compared to the corresponding grain legume monocultures (CV = 32%). Moreover, cereal-grain legume intercropping has higher yield stability than non-cereal-grain legume intercropping systems[45].

2.2 Efficient use of resources and saving mineral fertilizers

Nitrate is a problematic contaminant in agricultural regions and nitrous oxide (N_2O) is a greenhouse gas, and both are derived mainly from excess fertilizer N use[46,47]. Intercropping reduces the inputs of nitrogen fertilizers through the efficient use of resources[11] and further reduces ammonia volatilization and NO and N_2O emissions (Fig. 1(b)). A meta-analysis shows that 376 of 409 values of fertilizer nitrogen equivalent ratio (FNER) were > 1 (92%), indicating that intercropping achieved not only high yields but also high nitrogen use efficiency[48]. In intercropping systems with maize the FNER was higher than that of intercrops without maize, indicating that intercrops with maize save more N fertilizer compared with monocultures and intercrops without maize[49]. Legumes can fix N_2 and reduce mineral fertilizer input in legume-based intercropping (Fig. 1(b)). Also, legumes fix more nitrogen (per plant) when they are intercropped with cereals because cereals have higher competitive ability for nitrogen[48]. Reducing the input of nitrogen fertilizer can alleviate the impact of nitrate and nitrite on soils and reduce NO and N_2O emissions[46]. A recent study compared the N_2O emission ratio (N_2O emission amount/N applied) in monocultured maize and soybean and maize-soybean intercropping and found that the N_2O emission ratio of the intercropping was the lowest and that of monocultured maize was the highest[17]. Intercropping of deep-rooted (maize) and shallow-rooted (pepper) plants increased nutrient acquisitions and N use efficiency and thus reduced nitrate leaching losses[47].

Phosphorus is a limited and non-renewable resource and the overuse of P has led to increasing accumulation of P in soils, low P use efficiency in agriculture and high environmental risk[50]. A field experiment in northwest China shows that maize-turnip (*Brassica rapa*), maize-faba bean, maize-chickpea and maize-soybean intercropping systems explored the biological potential for efficient acquisition of P toward a sustainable and productive agroecosystem[18]. In maize-faba bean intercropping, the P acquisition of both intercropped faba bean and maize accumulated more than that of their corresponding monocultures, with the average P acquisition of intercropped faba bean increasing by 42.4% compared to monocultured faba bean at the start of flowering[51]. Compared with monoculture, the average apparent recovery of fertilizer P of the intercropping systems increased from 6% to 30% at 40 $kg \cdot ha^{-1}$ P and from 5% to 14% at 80 $kg \cdot ha^{-1}$ P on average over three years[18].

2.3 Pest and disease management: reducing pesticides

Plant diversity improves pest control through movement patterns, host associations, and predation which provide a prominent and sustainable management tactic[52]. A meta-analysis shows that high-diversity cropping systems have greater abundance (or occasionally richness) of natural enemies and herbivore mortality than low-diversity cropping systems[53]. Maize-legume intercropping and push-pull technology were effective in management of stemborer and fall armyworm in Africa, and intercropping maize with leguminous crops significantly reduced the severity of stemborer and fall armyworm compared to monocultured maize[54].

Panicle blast severity was ~ 20% in monocrops of glutinous cultivars but was reduced to 1% in mixed populations of glutinous and hybrid rice cultivars[55]. Compared with monocultured potatoes, potatoes (*Solanum tuberosum*) intercropped with maize reduced the adult and larva populations and reduced the damage from potato tuber moth by enhancing the number of parasitoids and the level of parasitism, and two rows of potatoes intercropped with three rows of maize showed the greatest population of parasitoids and parasitism[56]. Severity of northern maize leaf blight in intercropped plots was decreased significantly by 17% and 20%, 56% and 50%, and 30% and 23% in maize-tobacco (*Nicotiana alata*), maize-sugarcane (*Saccharum officinarum*) and maize-potato intercropping systems in two years, and the severity of broad bean (*Vicia faba*) chocolate spot disease declined by 34% when broad bean was intercropped with wheat[57].

2.4 Mitigating climate change and controlling soil pollution

Soil fertility and carbon sequestration impact global climate change, maintain soil fertility and reduce carbon emissions in agriculture and may thus alleviate global warming[58,59]. Soil fertility, including physical, chemical and biological properties, directly or indirectly affect plant productivity, water and air quality[60]. Higher plant species diversity increased soil carbon and nitrogen stocks compared with monocultures via greater root biomass accumulation in a perennial grassland[61]. High biodiversity led to increased carbon storage in roots and soil, and increased biomass yields will mitigate climate change if the biomass displaces fossil fuel use[59]. A long-term field experiment established in 2003 shows that soil organic C content and soil organic N content in intercropping were greater than in monoculture[62]. In maize-wheat, maize-rape (*Brassica napus*), and maize-pea intercropping systems, intercropping produced more grain yield versus monocultures and emitted 50% less C per ha per mm of water on average compared with the maize monoculture[63]. Maize silage is an important feedstock for biogas production. The global warming potential of maize-forage sorghum intercropping was 7.3% lower than maize silage, and forage sorghum-maize intercropping thus had lower environmental impact compared with monocultured maize, providing a promising alternative to maize silage for biogas production[64].

Contamination of soils with potentially toxic elements in agroecosystems is a critical issue affecting food security and food safety worldwide. Cd, Cr, Cu, Hg, Pb and Zn are the most common potentially toxic metals in contaminated soils[65] that lead to environmental degradation and inhibit plant growth[66]. Compared with monoculture, faba bean intercropping with *Sedum alfredii* inoculated with a plant growth promoting endophyte increased biomass as well as Cd and Pb concentrations in associated plant species, thus enhancing the Cd and Pb removal efficiencies[66]. Also, intercropping reduced Cd and Pb concentrations in faba bean to within the permissible range (0–0.2 $\mathrm{mg \cdot kg^{-1}}$, FW)[66].

2.5 Increasing above- and below-ground biodiversity of other taxa at field scale

Pollination is an ecosystem service that is critical to crops. Honey bees and wild pollinators (e.g., flies, beetles, moths, and butterflies) provide substantial pollination services[67]. Strong evidence shows that increasing plant diversity increases pollinators[68]. A field experiment found that increasing plant species richness significantly enhanced the functional diversity of pollinator communities and pollination services in grassland[69]. Great diversity of soil microorganisms and animals are essential in above-ground production and ecosystem functions such as litter decomposition and nutrient cycling[70].

Little attention has been paid to the effects of above-ground plant diversity on below-ground biodiversity. High plant species diversity can increase the diversity of mutualistic microfauna and other animal groups in soil through diverse litter quality, litter types or root exudates entering the soil[71]. A recent review shows that there is no general trend in the relationship between tree diversity and soil faunal diversity or abundance[70]. However, most studies did find that increased tree diversity or the addition of broadleaved trees to conifer stands had a positive effect on diversity or abundance of earthworms or soil microarthropods[70]. Wheat-clover intercrops significantly increased earthworm populations in terms of abundance and biomass compared to monocultured wheat[72]. A recent study shows that intercropping systems changed soil microbial community composition and increased the relative abundance of soil sordariales[73].

3 MECHANISMS UNDERLYING IMPROVED AGROECOSYSTEM FUNCTIONING OF INTERCROPPING

3.1 Contribution of complementarity and selection effects

There is a growing consensus that species diversity enhances ecosystem function in forest, grassland and agricultural ecosystems[42,43]. Several mechanisms have been proposed to explain the positive relationship between species diversity and ecosystem functions. Complementarity effects occur through either niche differences or facilitative interactions among species, resulting in greater resource acquisition and thus higher productivity[74]. Selection effects occur because polycultures have a higher chance of containing a single, productive taxon[75]. However, the relative strengths of complementarity effects and selection effects change across scales. A ten-year biodiversity experiment shows that complementarity effects increase while selection effects decrease through time[74]. Positive net biodiversity effects were attributed to complementarity effects at local scales but to selection effects at larger scales of space or time[76].

Complementarity effects are usually divided into niche differentiation and interspecific facilitation (Fig. 2). Above-ground niche differences are driven by light while below-ground niche differences are always driven by water and nutrient availability. Complementarity effects promoted positive biodiversity-productivity relationships in communities of young trees through increasing differences in vertical leaf niches and growth strategies between species[77]. In more diverse grassland plant communities, niche partitioning in water uptake via root distribution results in higher efficiency of water use[78]. Complementarity and selection effects may also be important mechanisms for overyielding of agroecosystems. In addition to niche complementarity, interspecific facilitation, via increasing nitrogen, phosphorus and micronutrient use efficiency, also has an important role in intercropping (Fig. 2). Here, we introduce the biodiversity effects of intercropping in terms of interspecific facilitation and niche differences (Fig. 3).

3.2 Interspecific facilitation in intercropping

Facilitative interactions (also known as abiotic facilitation) are usually defined as species differing in their ability to alter their habitat to benefit neighbors[79]. In steppe vegetation,

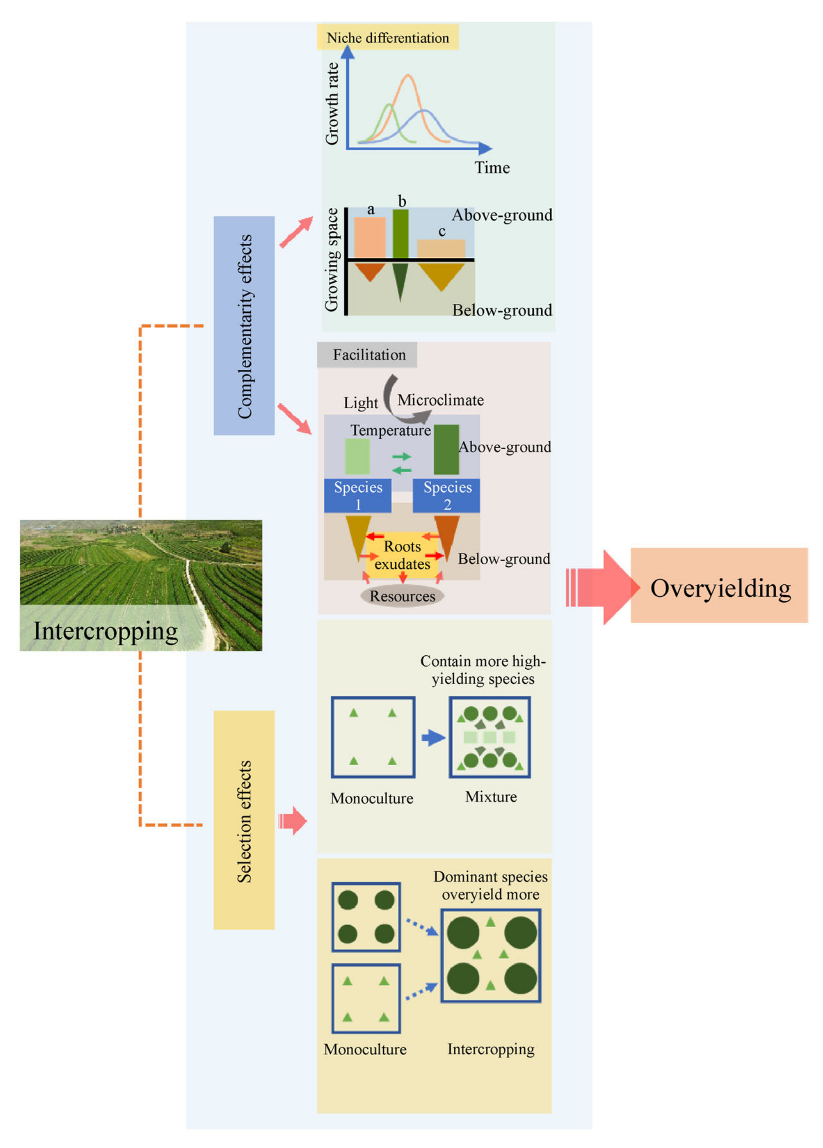


Fig. 2 The mechanisms of complementarity effects and selection effects driving overyielding in intercropping.

P-mobilizing species facilitated growth and increased P concentration of neighboring species, and this was a mechanism underlying a positive complementarity effect in P-limited communities[80]. Nurse species can benefit plant communities by relieving local abiotic stress and promote plant-microbe interactions[81]. Interspecific facilitation is caused mainly by the complementary use of resources, especially water, nitrogen and phosphorus in intercropping[15,82]. In arid and semiarid areas, intercropping often increases water availability or enhances water-use efficiency (WUE) through the spatial and temporal complementary of root distribution or shared mycorrhiza networks. For example, shallow-rooted species can access water from neighboring plant species with deep root systems[83]. Compared to monocultured maize, maize-cowpea intercropping increased crop cover and reduced soil moisture evaporation[84]. Pea-maize intercropping systems are widely used in northwest China, with intercropping increasing the WUE of maize but decreasing that of pea, and the effect of intercropping on WUE depends on the row arrangement of the intercropping system and shows high variability[15] (Fig. 3(f)).

Biological dinitrogen fixation is an efficient source of nitrogen for sustainable agricultural production (Fig. 3(b,e)). Biologically fixed nitrogen in legumes can be transferred to adjacent cereal

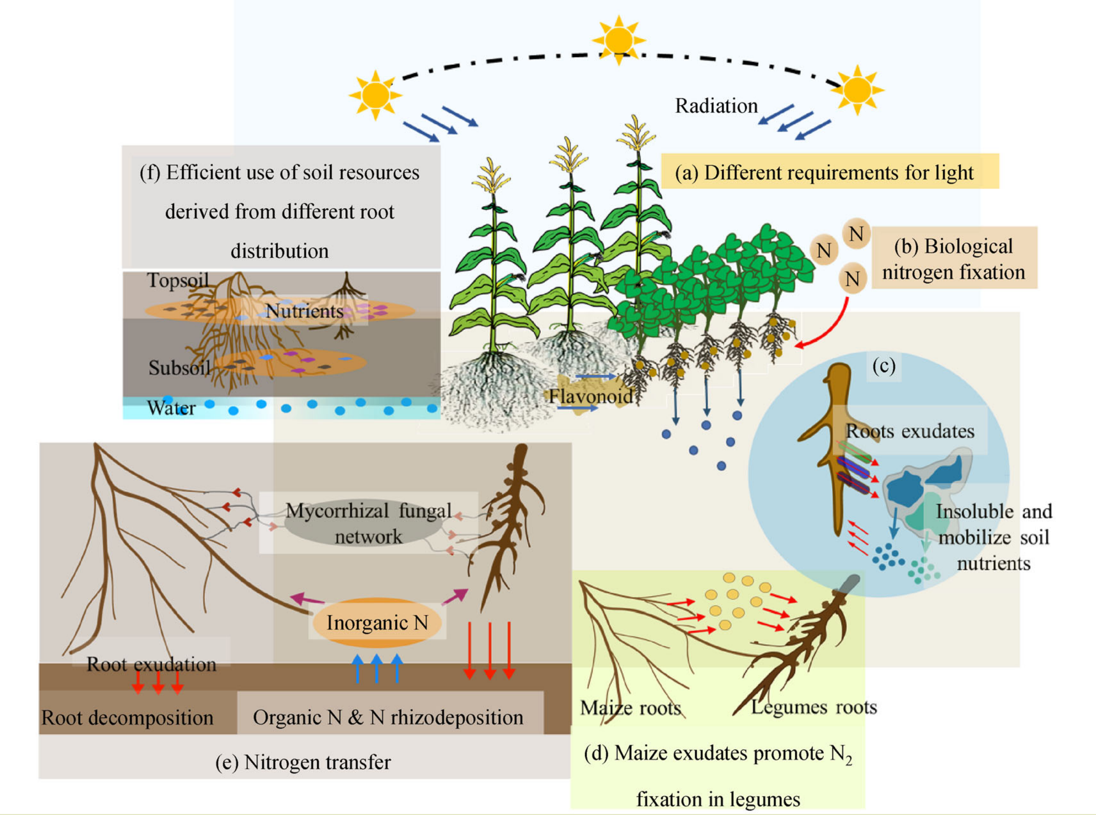


Fig. 3 Interspecific facilitation and niche differentiation increase resource use efficiency. (a) Differences in plant height and light requirement increase light interception and use efficiency. (b) Biological nitrogen fixation (BNF) of legumes reduces the nitrogen fertilizer input. (c) Root exudates of legumes increase the uptake of insoluble nutrients. (d) Root exudates from maize enhance faba bean nodulation and increase dinitrogen fixation. (e) Nitrogen transfer through root exudation, root decomposition and mycorrhizal fungal networks. (f) Differences in root distribution result in spatial complementarity.

crops in legume-cereal intercropping systems[85]. For example, nitrogen transfer from cowpea and lupin (*Lupinus micranthus*) to lettuce (*Lactuca sativa*) can be ~ 4 and 6 $kg \cdot ha^{-1}$, respectively[86]. Using the ^{15}N labeling method, nitrogen transfer from the rhizosphere of mung bean (*Vigna radiata*) to oat was 82 mg per plant, accounting for 16% of the total nitrogen content of oat. The amount transferred from the oat rhizosphere to mung bean was 38 mg per plant, accounting for nearly 9% of the total nitrogen content of mung bean[87]. Root-root interactions driven by maize root exudates stimulate nodulation and N_2 fixation by faba bean in maize-faba bean intercropping systems. A series of experiments shows that maize root exudates induce significant upregulation of expression of *CFI*, *NODL4*, *GH3.1*, *ENODL2*, *FixI* and *ENOD93* genes in faba bean roots, facilitating the nodulation of faba bean (Fig. 3(d))[75]. These results indicate that N facilitative interactions provide a potential explanation for a positive relationship between biodiversity and ecosystem productivity.

Phosphorus is an essential element to higher plants in many ecosystems. Some soils contain a large amount of P which is unavailable to most plant species[82]. Chickpea facilitates P uptake by intercropped wheat from an organic phosphorus source in a pot experiment with different root barriers. Compared with a solid root barrier where there were no interspecific root-root interactions, total P uptake by plants was 68% greater with mixed roots and 37% greater with a nylon mesh barrier[88] where the root-root interactions were full and partial, respectively, in maize-faba bean intercropping. Faba bean can release carboxylates, acid phosphatase and protons which increase soil P availability and improve the P nutrition of neighboring maize[88]. In cereal-legume intercropping system the interspecific below-ground interactions increase crop acquisition of soil P as follows: (1) different species require different forms of P, thus reducing competition for P between these plant species; (2) root exudates of legumes can promote the P acquisition of neighboring maize; (3) P acquisition is indirectly promoted by the activity of microbes in the soil[89]. When maize was grown with different intercrops under homogeneous or heterogeneous P distribution, localized P application or faba bean exudation increased P availability and increased shoot growth in maize in the maize-faba bean mixture[90]. Mobilization of sparingly soluble P by legumes benefited neighboring plants and increased P use efficiency with low-P fertilizers (Fig. 3(c)).

Iron, zinc, copper and other essential micronutrients of crops are involved in many essential physiological processes of plants. Compared to peanut monoculture, young leaves of peanut had higher chlorophyll content and HCl-extractable Fe concentrations in maize-peanut intercropping and the improved Fe nutrition of peanut in intercropping was mainly due to rhizosphere interactions between peanut and maize[91]. Recent advances have also demonstrated that peanut can take up Fe chelated by plant Fe-carriers and improve their Fe nutrition[92] (Fig. 3(c)). In chickpea-wheat intercropping, interspecific interactions increased the Fe contents in wheat and chickpea seeds by 1.26 and 1.21 times, and Zn concentration in chickpea seed by 2.82 times compared with monoculture. Improved Fe and Zn nutrition were also observed in guava (*Psidium guajava*)-sorghum or maize intercropping[93].

3.3 Niche differentiation in intercropping

Niche differentiation is considered to be a key driver for biodiversity enhancing ecosystem function in a diverse plant community[8]. Yu et al.[94] defined the index of temporal niche differentiation (TND) as the proportion of the total system time that component crops grow alone, and found that the LER of intercropping increases with TND. A recent meta-analysis shows that complementary effects increased with TND in maize-legume intercropping[95]. In wheat-maize and barley-maize intercropping in northwest China, wheat, barley and maize reached their peak daily nutrient uptake rates at different periods, with wheat and barley the dominant species at early co-growth stages, and the growth of maize was suppressed at early growth stages but recovered rapidly after the wheat or barely harvest. This study suggests that a temporal niche differentiation in nutrient use between these plants led to yield advantages of intercropping[96]. In oilseed rape-maize, oilseed rape-soybean and potato-maize intercropping, the time taken to attain maximum the daily growth rate was also different between intercropped species[97]. Maize-soybean relay intercropping is the main planting pattern in southwest China because of its high LER, and temporal differentiation in sowing and harvest dates increased nutrient use efficiency and led to overyielding of the whole intercropping system[17]. Altering the planting time of soybean in maize-soybean relay intercropping systems can reduce the competitive effect of maize on soybean, decreasing co-growth duration and increasing the grain yield of soybean via temporal niche differentiation[98].

Light is a limiting resource affecting many ecological processes in agroecosystems. Greater interception of solar radiation and higher use efficiency of light result in greater productivity in intercropping[99] (Fig. 3(a)). The dominant plant species (intercropped maize) had a similar radiation use efficiency (RUE) to monocultures, but the subordinate plant species (legumes) had greater RUE in intercropping than in monocultures, thus intercropping had greater RUE than monocultures and this may account for the yield advantage of intercropping[100]. Crop mixtures with different root distribution are able to occupy a larger niche space and thus can acquire more unexploited soil resources than monocultures[101]. In maize-faba bean intercropping the roots of maize usually spread under the faba bean rows[102]. Intercropped wheat altered its root length density and lateral root distribution under different N application regimes, while lateral root distribution of intercropped maize was less sensitive to N application regime[16]. High morphological plasticity of crop roots drives below-ground spatial niche complementarity and increases resource use efficiency of intercropping systems (Fig. 3(f)).

4 CONCLUSIONS

Intensive agriculture often pursues maximization of the productivity of monoculture with greater inputs of fertilizer, water and pesticides, and thus incurs substantial environmental costs. Intercropping is a traditional cropping system that has been practiced worldwide, especially in China, for thousands of years. Intercropping can contribute to food and livelihood security and potentially increase the long-term sustainability of food production with low environmental cost globally[29,43] (Fig. 4). This review summarizes strong evidence of the positive impact of crop diversification, especially intercropping on agroecosystem functions such as increasing yield and stability, increasing resource use efficiency, suppression of pests or diseases, reduction of carbon emissions and controlling soil pollution. The partition of complementarity and selection effects helps us better understand the mechanisms of spatial and temporal niche separation and facilitation in multiple cropping systems.

Intercropping practices are usually more labor-intensive than monocultures with fewer options for the use of machinery in intercropping. In addition, rural-to-urban labor migration has

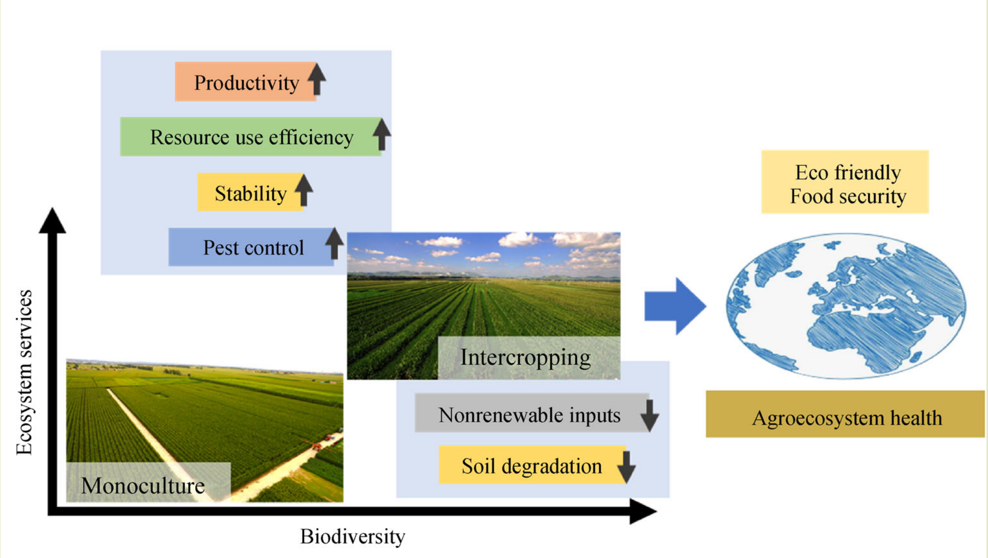


Fig. 4 Intercropping provides an alternative way to ensure food security and develop sustainable agriculture.

increased in China and, as a result, the development of intercropping is restricted due to the scarcity of rural labor and low degree of mechanization. Existing farm machinery can be used if the strip-width is adjusted in strip intercropping. Appropriate crop combinations with maximization of complementarity are critical in achieving greater advantages of intercropping. Long-term intercropping experiments are needed to detect possible slow changes produced by intercropping over the long term and to reveal the sustainable development of intercropping.

Quantifying and evaluating soil health will be necessary for managing soil-ecosystem services. Soil-health indicators can be classified as physical, chemical or biological, while previous studies have usually focused on some of these properties. Soil health should be considered as an important principle that contributes to sustainable development goals rather than only a property to measure in intercropping[49]. Biodiversity can simultaneously maintain multiple ecosystem functions and services (multifunctionality) in natural ecosystems[103]. However, the relationship between intercropping and multifunctionality has not been assessed. Finally, models integrating climate, soil, crop species and genotype modules can help to reveal how interspecific interactions change under various climatic and edaphic conditions, and this is critical in evaluating productivity, sustainability, climate risk and resource use efficiency of intercropping systems on larger scales.

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Compliance with ethics guidelines

Hao Yang, Weiping Zhang, and Long Li 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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