PLANT SCIENCE TODAY
Vol x(x): xx–xx
https://doi.org/10.14719/pst.3976

eISSN 2348-1900

REVIEW ARTICLE

Intercropping strategies for abiotic stress tolerance and nutrient acquisition

Rana Choukri[1], Mostapha Maach[2]*, Abbderrahmane Rahhou[1], Mohamed Faize[3], Ali Skalli[1], Mustapha Akodad[1], Abdlmajid Moumen[1] & Mourad Baghour[1]

[1]Departement of Biology, Multidisciplinary Faculty, Mohammed I University 62 700, Nador, Morocco
[2]Research Institute in Horticulture and Seeds, University of Angers 49 100, Angers, France
[3]Laboratory of Plant Biotechnology, Ecology and Ecosystem Valorization, URL CNRST10 , Faculty of Sciences, University Chouaib Doukkali 24 000, El Jadida, Morocco

*Correspondence email - mostaphamaach12@gmail.com

Received: 25 May 2024; Accepted: 04 February 2025; Available online: Version 1.0: 04 June 2025

Cite this article: Rana C, Mostapha M, Abbderrahmane R, Mohamed F, Ali S, Mustapha A, Abdlmajid M, Mourad B. Intercropping strategies for abiotic stress tolerance and nutrient acquisition. Plant Science Today (Early Access). https://doi.org/10.14719/pst.3976

Abstract

Abiotic stresses, including drought, extreme temperatures, salinity and nutrient deficiencies, significantly reduce global crop productivity, posing major challenges to food security, particularly in arid and semiarid regions. Climate change intensifies these stresses, emphasizing the need for resilient agricultural systems. Intercropping has emerged as a sustainable strategy to mitigate these impacts by enhancing soil moisture retention, regulating root-zone temperatures and optimizing nutrient acquisition. For instance, legume-cereal systems like maize-pigeon pea improve drought resilience, while peanut-maize intercropping enhances iron (Fe) and phosphorus (P) nutrition in calcareous soils. Agroforestry practices, such as wheat intercropped with alfalfa, increase water use efficiency and reduce soil salinity. These approaches offer practical solutions for smallholder farmers to adapt to climate change while improving crop tolerance to abiotic stresses. This study evaluates various intercropping systems to identify optimal practices tailored to specific environmental conditions, supporting food security and sustainable agricultural practices. By promoting agricultural sustainability, intercropping provides a pathway to mitigate the effects of climate change and secure global food production.

Keywords: climate change; drought; intercropping; salinity; sustainability; tolerance

Introduction

Abiotic stresses such as drought, salinity and extreme temperatures are the most severe factors limiting plant growth and crop productivity worldwide. These stresses pose significant challenges to current agricultural systems, particularly in the context of climate change. Reports indicate that 70% of yield reductions are caused by abiotic factors such as drought and salinity, with climate change exacerbating their effects (1, 2). Global warming amplifies drought conditions by altering rainfall patterns, increasing evaporation rates and reducing water availability, especially in arid and semiarid regions. Furthermore, rising temperatures affect agriculture by modifying cropping seasons, increasing irrigation demands and intensifying heat stress on crops (3). Salinity, in particular, is a major abiotic stress limiting crop productivity in these regions (4, 5), with estimates showing that at least 900 million hectares, or 7% of the world's total land area, are affected (6).

Drought, characterized by an extended water shortage caused by insufficient precipitation, significantly affects soil moisture, water availability and overall ecosystem balance. This reduction in soil humidity disrupts plant growth and the water cycle. Tools like the standardized precipitation index (SPI) and Palmer drought severity index (PDSI) are commonly used to assess the severity and duration of droughts by measuring deviations in precipitation and soil moisture compared to historical data (7).

During drought, water loss intensifies due to increased evaporation and transpiration. Evaporation removes water from the soil and other surfaces, while transpiration releases water into the atmosphere through plant processes. Under arid conditions, high evaporation rates significantly reduce soil moisture, amplifying the effects of drought. At the same time, plants may increase water uptake through transpiration, further depleting soil water reserves. The FAO-56 Penman-Monteith equation is widely used to calculate evapotranspiration and determine crop water needs (8, 9). The expansion of drought-affected regions is closely linked to rising global temperatures, which accelerate evaporation and transpiration rates. These processes rapidly drain surface and soil water, creating a self-reinforcing cycle that exacerbates soil dryness and crop stress. In arid and semiarid areas, prolonged dry periods and reduced rainfall worsen the situation, as evaporation outpaces the replenishment of soil moisture. This cumulative impact heightens water scarcity and causes severe agricultural losses (10, 11).

Edaphic factors such as soil pH, relative water content (RWC), nutrient availability and water holding capacity (WHC) are critical in enhancing plant resilience against abiotic stresses like drought, salinity and heat. Soil pH influences nutrient availability and microbial activity, with most essential nutrients being optimally available in a pH range of 6 to 7. Extreme pH levels can lead to nutrient deficiencies or toxicities, while neutral pH conditions support microbial communities that enhance nutrient cycling and plant health (12). Similarly, RWC is a key indicator of a plant's hydration status and ability to tolerate water stress. Higher RWC ensures proper physiological processes, including photosynthesis and nutrient transport, allowing plants to maintain growth under drought and heat stress (13). Nutrient availability is equally vital for stress resistance, as macronutrients like nitrogen (N) and potassium (K) and micronutrients like selenium and zinc support metabolic processes and antioxidant production, which mitigate oxidative damage caused by abiotic factors (14).

Additionally, WHC contributes to drought resilience by enabling soils to retain moisture longer, providing a buffer against water scarcity. Soils with higher WHC also promote deeper root development, improving water and nutrient access, which enhances stress tolerance (15). Together, these edaphic factors create a supportive environment for plant growth under adverse conditions, emphasizing the importance of soil management in mitigating the effects of abiotic stresses.

Salinity refers to the amount of soluble salts in soil or water, which is crucial in determining soil health and plant growth. It is typically assessed by measuring a saturated soil extract's electrical conductivity (EC), expressed in deci Siemens per meter (dS/m) at a standard temperature of 25°C. Soils are categorized as saline when their EC exceeds 4 dS/m, a threshold that negatively impacts crop productivity (16).

Saline and sodic soils differ significantly in their salt composition, physical structure and effects on plant growth. Saline soils contain high concentrations of soluble salts, with EC values above 4 dS/m, a pH below 8.5 and an exchangeable sodium percentage (ESP) less than 15. The primary issue in saline soils is osmotic stress, which restricts water absorption by plant roots. In contrast, sodic soils are characterized by high sodium (Na) ion concentrations (ESP > 15), leading to poor soil structure due to the dispersion of clay particles, reduced water infiltration and an alkaline pH exceeding 8.5 (17, 18).

Salinization of agricultural soils arises from various factors, significantly affecting soil management and crop productivity. Continuous saline irrigation water causes salts to accumulate in the root zone, reducing soil fertility and inhibiting plant growth (19). Poor drainage systems can result in waterlogging, hindering salt leaching and worsening salinity (20). Overuse of chemical fertilizers also contributes to the accumulation of salts in the soil (21). Additionally, natural processes, including the weathering of salt-containing parent materials and the upwelling of saline groundwater, play a major role in this process (22). Arid and semiarid regions are particularly susceptible due to limited rainfall and high evaporation rates, which concentrate salts in the soil (16).

Salinization is an increasing concern, particularly in Africa and Asia, as it disproportionately impacts arid and semiarid regions. Globally, more than 833 million hectares of land, or 8.7% of the world's total land area, are salinity-affected. Of these, 85% are in arid zones such as deserts and steppes. Countries like Sudan and Egypt are particularly affected in Africa, while heavily irrigated nations such as India and Pakistan face similar challenges in Asia. Moreover, between 20% and 50% of irrigated soils in these regions are salinity-contaminated, threatening food production for over 1.5 billion people worldwide (23) (Fig. 1). In Africa, salinity and drought affect over 40 million hectares of arable land annually, contributing to an estimated 15-20% reduction in crop yield, particularly in regions like the Horn of Africa and North Africa. In Asia, drought affects more than 30% of agricultural areas, with salinity impacting over 60 million hectares, causing yield losses valued at billions of dollars each year (23, 24). Alongside salinization, severe water stress caused by drought is another pressing issue. In Africa, 44% of agricultural land experiences water scarcity, with millions reliant on farming heavily impacted. This issue is especially dire in areas such as the Horn of Africa, where repeated droughts have led to significant agricultural losses and escalating food insecurity. Similarly, between 25% and 30% of agricultural land in Asia is severely affected by drought, particularly in countries such as India and China, where prolonged dry periods disrupt water resources and crop yields (24).

In addition to drought and salinity, soil and crop canopy temperatures influence plant growth and production (25, 26). Sustainable farming techniques, such as intercropping, have been identified as effective strategies to mitigate the effects of abiotic stresses. Intercropping systems enhance crop performance by improving physiological and biochemical traits, particularly under stress conditions (27). Additionally, diversifying cropping systems aids in managing year-to-year climate variability and supports the resilience of agricultural systems (28). For example, (29) demonstrated that strip intercropping maize with alfalfa significantly improved production compared to monocropping systems (Fig. 2).

Intercropping also contributes to biotic stress management, protecting against pests, diseases and yield losses (30). Crop mixtures enhance genetic and species diversity within agroecosystems, which helps control pests and diseases (31). Furthermore, intercropping is a sustainable alternative for improving plant nutrient absorption, surpassing methods like rhizosphere fertilization and intensive water management (32). However, implementing effective intercropping systems requires careful selection of compatible crop species to minimize competitive inhibition while maximizing agronomic and economic benefits. This review explores the various roles of intercropping systems in addressing food and environmental security challenges. It also evaluates intercropping's contributions to nutrient acquisition, crop tolerance to abiotic stresses and sustainable agricultural practices.

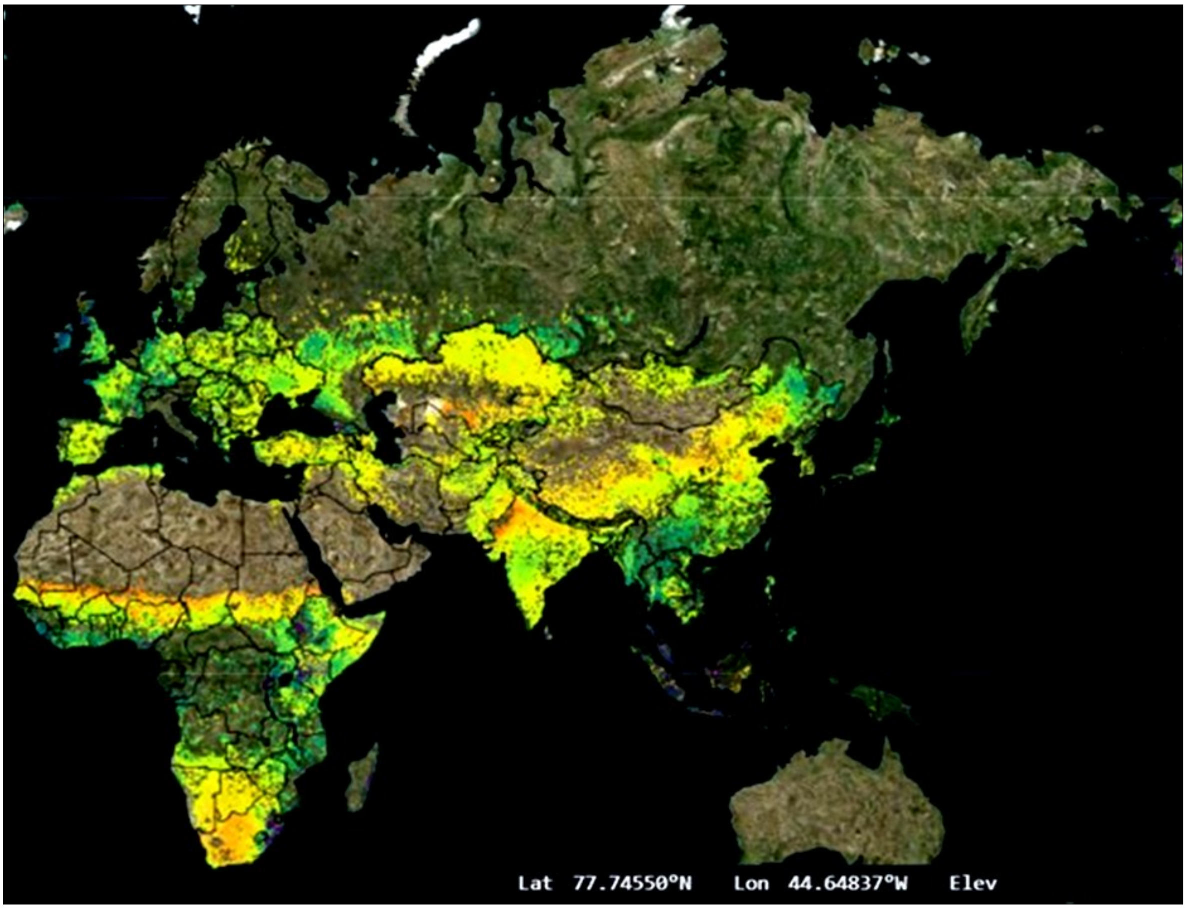

Fig. 1. The map shows different colors representing soil salinity levels, based on conventions commonly used for this type of representation. Green indicates areas with low salinity or non-salinized soils, while yellow corresponds to moderate salinity. Orange signals high salinity, often associated with degraded or at-risk areas. Red/purple regions are those severely affected by salinization, reflecting a critical level of degradation. Finally, blue may represent irrigated areas or groundwater influencing soil salinity.

Methodology

The methodology of this article is based on a comprehensive analysis of different intercropping strategies and their role in abiotic stress tolerance, including drought, salinity, extreme temperatures and nutritional deficiencies. We conducted an exhaustive review of the scientific literature to identify relevant research regarding the effect of intercropping on tolerance to various abiotic stresses. We examined experimental studies conducted on various crops and diverse environments to understand the underlying mechanisms involved in plant responses to these stresses.

Furthermore, we investigated various intercropping practices, such as strip intercropping, row intercropping, mixed intercropping and relay intercropping, to determine the advantages and limitations of each approach in terms of abiotic stress tolerance. We also evaluated the impact of planting density and specific genotype combinations on abiotic stress tolerance within the framework of intercropping. Finally, we synthesized the results of the reviewed studies to provide practical recommendations to farmers and policymakers on the effective use of intercropping to enhance crop resilience to abiotic stresses in the context of climate change.

Additionally, we highlighted key terms such as tolerance, salinity, climate change, temperature, water stress and intercropping as keywords in this article review.

Results

Role of intercropping in abiotic stress tolerance

Drought tolerance: Drought remains one of the most pressing challenges to plant growth and agricultural productivity. Predictions indicate that the frequency and severity of extreme drought events will increase, presenting significant risks to ecosystems worldwide (33). Global warming exacerbates drought conditions by altering rainfall patterns, increasing evaporation rates and reducing water availability, especially in arid and semiarid regions (1, 3). These changes heighten water stress on crops, further compounding the challenges posed by drought (10, 11). Intercropping has emerged as a viable (Fig. 2 and Table 1) and sustainable approach that can boost crop yields, offer natural shading and efficiently use water resources (34). Despite the higher planting density in intercropping systems compared to monoculture maize and the potential for increased competition for water, these systems do not show a greater tendency for drought-induced yield reduction (35). In areas with ample water availability, intercropping has significant potential to meet the demands of high-yield monoculture systems (36). This technique also minimizes water loss through evaporation. It has been widely adopted to mitigate wind erosion, increase water and light use efficiency and create a more favorable soil moisture environment for crop development (37).

Fig. 2. Intercropping of tomato with maize was carried out at the Multidisciplinary Faculty of Nador (Morocco) (Photo taken by Mourad Baghour).

Previously, a study showed that in the semiarid region of India and under uneven and deficit rainfall situations, the production of the soybean/pigeon pea intercropping system is higher than in monoculture of either soybean or pigeon pea (38) (Table 1). In temperate environments, the wheat-soybean (*Triticum aestivum* L.-*Glycine max* L. Merr.) double-crop system often improves radiation and water's capture and use efficiency and exploits a greater fraction of the potential environmental productivity (39). Recent studies have highlighted the development of environmentally friendly planting methods, such as sole forage cropping and forage intercropping, for forage production (40). The authors demonstrated that strip intercropping of spring wheat and alfalfa can serve as an effective and sustainable strategy in arid regions, enhancing irrigation water efficiency, increasing grain and forage yields and boosting net income.

It has been reported that intercropping is crucial in improving physiological and biochemical traits under drought conditions (27). Maize-pigeon pea intercropping can produce the same amount of food on less land in drought and non-drought scenarios without reducing the drought resilience of low-input smallholder maize systems (35). The benefits of maize-pigeon pea intercropping over monocultures during drought may also stem from its positive effects on soil hydrology and fertility. It was reported that intercropping and N addition influenced the transcript levels of six genes responsible for encoding enzymes in the non-enzymatic antioxidant cycle (34). The genotype-specific interactions observed in intercropping underscore the importance of selective breeding focused on creating well-suited cultivars for maize and potato intercropping. Additionally, it was shown that below-ground interactions may play a more significant role than above-ground interactions, with potatoes exhibiting a stronger competitive ability than maize when intercropped (41).

Moreover, the rhizosphere microbiome can significantly influence plant health by improving plants' tolerance to abiotic stress (42). Wheat-maize intercropping has been shown to outperform monocropping in physiological, biochemical and molecular traits under rain-fed, water-limited conditions. Intercropping led to notable improvements in chlorophyll fluorescence and gas exchange parameters such as Fo/Fm, PS-II efficiency, photosynthesis, stomatal conductance, carbon capacity and the activities of antioxidant enzymes

Table 1. The agronomic benefit of different types of intercropping systems for plants grown under drought stress.

Intercropping system	Country	Agronomic benefits	References
Maize-Pigeonpea	Tanzania	Enhanced land use efficiency.	(35)
Jujube/Cotton	China	Reduced soil temperature and evapotranspiration, improved water-use efficiency.	(37)
Soybean-Pigeonpea	India	Increased yields from soybean and pigeon pea and enhanced drought tolerance.	(38)
Wheat-Soybean	Argentina	Increased grain yield and glucose. Enhanced economic and environmental outcomes. Improved spatial and temporal diversity.	(39)
Spring wheat-Alfalfa	China	Increased irrigation efficiency. Improved forage yield.	(40)
Winter faba bean-Winter wheat	Germany	Increased the yield of winter faba bean, optimized water resource use and finally enhanced drought tolerance.	(43)

compared to monocropping systems (27). Regulating osmotic adjustment under water stress is a key factor in drought tolerance. In many plant species, the buildup of compatible osmolytes like proline and sugars is a vital strategy for enhancing drought resilience (43, 31). Under drought stress, the upregulation of the proline synthesis gene P5CR1 and the proline degradation gene ProDH downregulation led to proline accumulation (27). A genetically modified drought-tolerant sugarcane variety was shown to secrete and accumulate substantial rhizosphere and soil nutrients, contributing to a distinct rhizosphere bacterial community in soybean intercropped with drought-tolerant sugarcane, compared to those intercropped with wild-type sugarcane (43). Recent reports indicate that intercropping treatments significantly boost antioxidant capacity by enhancing the activities of enzymes like superoxide dismutase, peroxidase, catalase and ascorbate peroxidase while simultaneously reducing lipid peroxidation by lowering malondialdehyde (MDA) levels (43). In studying the effects of intercropping on specific secondary metabolites, it was found that certain health-promoting phytochemicals, such as glucosinolates, can be enhanced through intercropping systems (27). Additionally, intercropping has been identified as an effective strategy for managing drought stress by boosting carotenoid concentrations and improving water-use efficiency.

Temperature Tolerance

Mediterranean agriculture faces major climate change and sustainability challenges. Global warming and climate change are causing an alarming increase in the frequency and intensity of different abiotic stresses, such as heat and cold waves. Changes in soil and canopy temperatures could negatively affect plant growth and crop productivity (25). The intercropping system is a cheap and simple alternative that helps to reduce the ambient temperature (44). Soil temperature changes depend on atmospheric temperature fluctuations and are impacted by cropping systems. The soil temperature stability of intercropping is significantly higher than that of monocropping (Table 2). Suitable soil temperature aids gas exchange between the soil and the atmosphere, enhances microbial activity from the soil and enhances root activity (37).

Intercropping systems create a more favorable microenvironment for plant growth by mitigating temperature extremes, conserving soil moisture and enhancing light interception (Table 2). In faba bean-wheat intercropping (45), intercropping improves the microclimate by reducing relative humidity while increasing canopy temperature and light transmittance (46). Similarly, during the summer, the extensive canopy of a main crop like cotton (Jujube-Cotton intercropping)(47) reduces air movement and temperature, which decreases evaporation and raises relative humidity (48). Intercropping systems can lower light-intensity air and soil temperatures while enhancing the plants' capacity to capture radiation energy (Table 2).

Conversely, intercropping can reduce sunlight intensity and air temperature while increasing canopy humidity (46). In safflower-chickpea intercropping (49), the canopy temperature was reduced by 2.17°C and 2.88°C for safflower and chickpea, respectively, due to the shading provided by safflower. This reduction was attributed to increased land coverage, improved soil moisture retention, reduced soil surface evaporation, enhanced water use efficiency and higher canopy humidity (50). Research on the mitigating effects of multi-variety intercropping and mixed cropping during the flowering stage has shown that high-temperature tolerance is significantly improved through appropriate variety combinations and row-spacing adjustments (51). In arid regions, agricultural practices that reduce surface soil temperature, such as increasing canopy density, straw mulching and intercropping, can lower soil respiration and boost grain yield (52). It was concluded that soil amendment with raw garlic stalk significantly reduced malondialdehyde content in eggplant leaves, demonstrating the potential of garlic-based strategies to enhance the antioxidative defense system and mitigate oxidative stress in monocropped eggplant (53), which can lessen the damage to eggplant and enhanced the plants' resistance to high temperatures and other stresses (54).

Salinity tolerance

Salt stress significantly affects plant growth and crop productivity, especially in arid and semiarid regions, where soil salinity seriously threatens food security (43). Over 39% of the world's drylands are impacted by saline soils in various

Table 2. The agronomic benefit of different types of intercropping systems for plants grown under temperature stress.

Intercropping system	Country	Agronomic benefits	References
Sweet corn-Cauliflower	Indonesia	Reduced the air temperature of the cauliflower canopy. Increased leaf area, dry weight and yield of cauliflower plants.	(44)
Faba Bean-Wheat	China	Increased the yield of wheat and faba bean. Increased the canopy temperature and transmittance of light.	(45)
Faba Bean-wheat	China	Increased the yield of wheat and faba bean. Increased the canopy temperature and transmittance of light.	(46)
Jujube-Cotton	China	Stabilized soil temperature. Reduced water loss by evaporation. Increased cotton crop yield.	(47)
Jujube-Cotton	China	Reduced root zone temperature under jujube and cotton.	(48)
Safflower-Chickpea	Iran	Increased leaf area index and chlorophyll content. Improved received light percentage and canopy temperature.	(49)
Safflower-Chickpea	Iran	Increased leaf area index and chlorophyll content Enhanced received light percentage Improve canopy temperature.	(50)
Garlic stalk with Eggplant	China	Reduced malondialdehyde content in eggplant leaves, enhanced antioxidative defense system, mitigated oxidative stress in monocropped eggplant.	(53)

subhumid, semiarid and arid regions (55, 56). Salinity is a major abiotic stress limiting crop productivity in these regions, with estimates showing that at least 900 million hectares, or 7% of the world's total land area, are affected (6). The limited rainfall and high evaporation rates in these areas exacerbate salt accumulation in the soil, further intensifying the impact of salinity (16). These conditions significantly hinder crop productivity and soil health, especially in arid and semiarid regions where water scarcity compounds the challenges posed by salinity (23). Intercropping, a traditional agricultural system (Table 3), is vital in such resource-limited environments, offering efficient resource use and resilience against abiotic stresses, including salinity (57). Cropping patterns influence soil salinity, particularly their effects on water balance and leaching processes during intercropping periods (58). Additionally, intercropping can improve soil nutrient status and regulate Na/K homeostasis, enhancing salt tolerance in peanuts (59).

Research has demonstrated the benefits of various intercropping systems for improving soil salinity and enhancing crop resilience to salt stress. In the hulless barley-pea mixed-cropping system, N and P application rate adjustments influence rhizosphere soil microbial diversity, potentially enhancing nutrient use efficiency and biomass production (60). The wheat-mustard intercropping system improves growth and photosynthetic performance in India, contributing to enhanced crop productivity and efficient resource utilization, as observed under controlled conditions (61). In another context, in Tunisia, combining salt-sensitive tomato plants (*Solanum lycopersicum* L.) with the salt-tolerant halophyte *Arthrocaulon macrostachyum* proved effective in reducing soil salinity and boosting tomato productivity. This strategy also optimized water use, mitigated osmotic stress and stabilized growth hormone levels in tomatoes, making it a sustainable solution for reclaiming saline soils (62). Shifting focus to China, intercropping soybean (*Glycine max*) with *Suaeda salsa* in saline soils promoted soybean development by lowering salt stress, balancing ion concentrations in the soil and enriching the rhizosphere microbial community. This approach significantly enhanced soybean biomass and reduced Na levels in the roots, presenting a valuable method for increasing crop performance under saline conditions (63).

Similarly, in Italy, salt-sensitive lettuce (*Lactuca sativa* L.) was intercropped with salt-tolerant *Salsola soda* in a hydroponic system, which improved the nutritional profile of *S. soda*. However, this system heightened abiotic stress on lettuce by intensifying resource competition for light and CO_2, underscoring its limitations under specific salinity levels (64).

In Iran, a mixed cropping system involving *Kochia scoparia*, *Sesbania aculeata* and *Cyamopsis tetragonoliba* demonstrated considerable physiological and yield improvements under saline irrigation. This practice enhanced K uptake, reduced cell damage and improved salt resilience, particularly for *Kochia*, which thrived under high salinity (65). Meanwhile, in India, combining bioinoculants with intercropping reduced the impact of salinity and drought

Table 3. The agronomic benefit of different types of intercropping systems for plants grown under salinity stress

Intercropping System	Country	Agronomic Benefits	References
Sweet Basil-Jatropha	India	Increased the yield. Enhanced land use efficiency. Stimulated the biological activity in the rhizosphere soil. Improved soil properties in terms of soil pH, electric conductivity and organic carbon.	(56)
Peanut-Maize	Turkey	Rhizosphere chemistry improvement by peanut root. Decreased the concentrations of Na in the shoots of maize and barley. Improved Fe, Zn and Mn nutrition of peanut.	(58)
Peanut-Sorghum	China	Improved soil nutrient status and increase salt tolerance, Regulated sodium/K homeostasis in peanut.	(59)
Hulless Barley and Pea mixed	China	Improved nitrogen and phosphorus application enhances rhizosphere microbial diversity, promoted better soil health and nutrient efficiency.	(60)
Wheat-Mustard	India	Improved growth and photosynthetic performance of wheat and mustard, leading to enhanced resource utilization and crop productivity in intercropping systems.	(61)
Tomato (*Solanum lycopersicum*) and *Arthrocaulon macrostachyum*	Tunisia	Reduced soil salinity, improved tomato productivity, optimized water use, mitigated osmotic stress.	(62)
Soybean (*Glycine max*) and *Suaeda salsa*	China	Enhanced soybean biomass, reduced sodium content in roots and improved rhizosphere microbial diversity.	(63)
Lettuce (*Lactuca sativa*) and *Salsola soda*	Italy	Improved nutritional quality of *S. soda* , but increased abiotic stress on lettuce.	(64)
Kochia scoparia, Sesbania aculeata and Cyamopsis tetragonoliba	Iran	Increased leaf K, reduced cell damage and improved salt tolerance, particularly for Kochia.	(65)
Bioinoculants and intercropping systems	India	Mitigated salinity and drought stress and promoted sustainable agriculture through soil microbe-plant interactions.	(66)
Maize (*Zea mays* L.) and Legumes	South Africa	Improved soil organic matter, ammonium and nitrate levels, reduced bulk density and enhanced soil fertility.	(67)
Maize (*Zea mays* L.) and *Suaeda salsa*	China	Enhanced salt accumulation around *S. salsa* roots, reduced nutrient competition, boosted maize growth.	(68)
Peanut (Arachis hypogaea) and Sorghum (*Sorghum bicolor*)	China	Improved rhizosphere soil properties, enhanced enzymatic activity and microbial diversity under saline stress.	(69)
Peanut-Sorghum	China	Increased the production of metabolites responsible for stress tolerance.	(73)

stress while supporting sustainable farming practices. This technique enhanced plant resilience through beneficial interactions between soil microbes and crops, highlighting its potential for restoring degraded lands (66).

Turning to South Africa, intercropping maize (*Zea mays* L.) with legumes like chickpea and mung bean improved soil health in both rainfed and irrigated settings. The system increased organic matter, ammonium and nitrate levels while decreasing soil bulk density, showcasing the soil fertility benefits of legume integration (67). In China, intercropping maize with *Suaeda salsa* further demonstrated its utility by enhancing salt accumulation around the halophyte's roots and reducing nutrient competition. The application of nitrate N further boosted maize growth and improved the system's efficiency in rehabilitating saline soils (68).

Finally, intercropping peanuts (*Arachis hypogaea*) with sorghum (*Sorghum bicolor*) in China also demonstrated transformative effects on soil properties and microbial diversity under saline stress. This approach enhanced enzymatic activity, soil nutrient content and microbial structure, ultimately improving peanut yield and environmental adaptability (69).

These intercropping systems highlight the potential of combining halophytes with traditional crops, promoting soil desalination, improving mineral nutrition and increasing yields. For example, halophytes like *Salicornia* and *Arthrocaulon* absorb salts from the soil, enhancing soil desalination and boosting crop yields (70, 71). Intercropping with these plants also triggers various metabolic and signaling pathways that help crops adapt to saline conditions, such as enhanced sugar metabolism and the accumulation of protective metabolites (72). Furthermore, it has been shown to increase the production of metabolites responsible for stress tolerance (73).These findings demonstrate the effectiveness of intercropping systems in mitigating the adverse effects of salinity and improving agricultural productivity in saline-prone areas.

Nutrient Deficiency Tolerance

Diversified cropping systems, including crop rotation and intercropping, are commonly employed to enhance the nutritional status of various plant species. Intercropping is a promising strategy to increase resource use efficiency and reduce carbon emissions, contributing to the sustainability of agriculture (74). Soil pH, a critical edaphic factor, plays a pivotal role in nutrient availability and microbial activity, as most essential nutrients are optimally available in a pH range of 6 to 7 (12). Neutral pH conditions further support microbial communities that enhance nutrient cycling and plant health (13), providing a foundation for intercropping systems to thrive.

Recent findings indicate that the increase in crop productivity in alternate intercropping systems is linked to enhanced canopy photosynthesis and nutrient uptake by root systems associated with rhizosphere microbes (75). In these systems, root interactions between species reduce competition through spatial and temporal differentiation in root distribution while facilitating the uptake of nutrients such as N, P and micronutrients (76). Intercropping between grasses and dicots has been shown to impact the availability of micronutrients in the rhizosphere of both species (77). For example, Fe deficiency chlorosis in peanuts can be alleviated by intercropping with maize in calcareous soil (78). These researchers observed that intercropping altered Fe concentration, pH, Olsen-P and N levels in the peanut rhizosphere at various growth stages, playing a key role in regulating Fe nutrition in peanuts grown in calcareous soils (79) (Table 4).

Similarly, changes in rhizosphere processes, such as Fe availability, pH and Olsen-P, could enhance Fe nutrition in intercropped peanuts (80). Peanut/maize intercropping also boosted the uptake of Zn, P and K in peanut shoots and Fe and Zn content in peanut seeds (81). Likewise, maize/peanut intercropping improved peanut's Fe nutrition (Table 4).

The enhancement of Fe nutrition in dicots, particularly those prone to Fe deficiency under stress, through intercropping with grasses, may result from root interactions and the creation of favorable rhizosphere conditions by grass exudates. Intercropping facilitates the mobilization and absorption of K, P and micronutrients via rhizosphere interactions, improved soil micro-ecology and increased microbial populations and enzyme activity in the soil, which are critical for higher crop yields (79).

Legume-cereal intercropping is gaining interest worldwide as a method to optimize mineral resource use. In these systems, increased crop functional diversity stimulates root/rhizosphere activities, leading to greater microbial diversity and promoting morphological and biochemical changes that improve shoot biomass and nutrient uptake (82). For example, plants capable of mobilizing P facilitated the conversion of sparingly soluble inorganic P in the soil by releasing carboxylates, protons, or enzymatically hydrolyzing organic P via root or microbial phosphatase enzymes, making P available to intercropped plants lacking this capability (72).

Table 4. The agronomic benefit of different intercropping systems for plants grown under nutrient deficiency

Intercropping system	Country	Agronomic benefits	References
Tomato with the halophyte *Arthrocaulon macrostachyum*	Spain	Stimulated sugar and starch metabolisms in tomato.	(71)
Maize-Peanuts	China	Increased the expression of *AhFRO1* and *AhYSL1* genes. Improved the iron nutrition of peanuts in calcareous soils.	(78)
Chinese Milk Vetch-Rape	China	Improved soil microbial community in rhizosphere.	(80)
Cotton-Peanut	China	Increased productivity via enhanced canopy photosynthesis and nutrient uptake.	(82)

By analyzing the effect of cotton-maize intercropping on rhizosphere properties, P bioavailability and the expression of key genes involved in P availability, it was concluded that intercropping increased P bioavailability by altering rhizosphere microbial composition and functional gene expression (73). Additionally, compared to monoculture, alternate intercropping boosted N uptake by 8.8%, P by 10.9% and K by 8.5% in cotton and 6.4%, 9.2% and 8.8%, respectively, in peanuts (78). Both alternate and traditional intercropping methods led to increased partitioning of 13C-labeled photoassimilate to reproductive organs.

Intercropping systems involving legumes also promote symbiotic N fixation, reducing N requirements by 26% without sacrificing yields (83). A study on the response of soil microbial genes involved in N cycling in intercropping systems revealed that the abundances of ammonia monooxygenase genes, such as archaea-amoA in ammonia-oxidizing archaea and nitrogenase Fe protein (nifH), were significantly higher in intercropping systems, thereby promoting N transfer from soil to crops, increasing N use efficiency and lowering nitrous oxide (N_2O) emissions (44). Moreover, intercropping influences the accumulation of minerals and secondary metabolites, which can affect the nutritional quality of crops through interspecific competition and complementation (78).

Conclusion

The intercropping system is a recently adopted strategy to enhance crop tolerance to biotic and abiotic stresses. Its effectiveness depends not only on the pedoclimatic conditions of each region but also on the specific crop combinations and the nature of the stress factors involved. Four primary intercropping patterns have been identified: i) strip intercropping, ii) row intercropping, iii) mixed intercropping and iv) relay intercropping. Additionally, factors such as plant density and specific genotype combinations play a critical role in optimizing the benefits of intercropping under varying stress conditions.

Acknowledgements

Mohamed Faize and Mourad Baghour were supported by funding from the ‘Ministère de l’Education Nationale, de la Formation Professionnelle, de l’Enseignement Supérieur et de la Recherche Scientifique (MENFPESRS, Morocco; Convention N-3) within the framework of the PRIMA Project (UToPIQ-PCI2021-121941).

Authors' contributions

MB proposed the idea and wrote this research article. MM revised the manuscript. CR, MF, MA, AS and AR read the article.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used Grammarly and Chat GPT in order to improve the language and grammar. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication

References

1. KhokharVoytas A, Shahbaz M, Maqsood MF, Zulfiqar U, Naz N, Iqbal UZ, *et al.* Genetic modification strategies for enhancing plant resilience to abiotic stresses in the context of climate change. *Funct Integr Genomics*. 2023;23:283. https://doi.org/10.1007/s10142-023-01202-0
2. Peleg Z, Reguera M, Tumimbang E, Walia H, Blumwald E. Cytokinin-mediated source/sink modifications improve drought tolerance and increase grain yield in rice under water-stress. *Plant Biotechnol J.* 2011;9(7):747-58. https://doi.org/10.1111/j.1467-7652.2010.00584.x
3. Ali S, Liu Y, Ishaq M, Shah T, Abdullah, Ilyas A, et al. Climate change and its impact on the yield of major food crops: evidence from Pakistan. Foods. 2017;6(6):39. https://doi.org/10.3390/foods6060039
4. Maach M, Baghour M, Akodad M, Gálvez FJ, Sánchez ME, Aranda MN, et al. Overexpression of LeNHX4 improved yield, fruit quality and salt tolerance in tomato plants (*Solanum lycopersicum* L.). Mol Biol Rep. 2020;47:4145–53. https://doi.org/10.1007/s11033-020-05499-z
5. Maach M, Rodríguez-Rosales MP, Venema K, Akodad M, Moumen A, Skalli A, et al. Improved yield, fruit quality and salt resistance in tomato co-overexpressing LeNHX2 and SlSOS2 genes. Physiol Mol Biol Plants. 2021;27:703–12. https://doi.org/10.1007/s12298-021-00974-8
6. Bijalwan P, Jeddi K, Saini I, Sharma M, Kaushik P, Hessini K. Mitigation of saline conditions in watermelon with mycorrhiza and silicon application. Saudi J Biol Sci. 2021;28:3678–84. https://doi.org/10.1016/j.sjbs.2021.05.019
7. Alharbi S, Felemban A, Abdelrahim A, Al-Dakhil M. Agricultural and Technology-based strategies to improve water-use efficiency in arid and semiarid areas. Water. 2024;16(13):1842. https://doi.org/10.3390/w16131842
8. Benos L, Tagarakis AC, Dolias G, Berruto R, Kateris D, Bochtis D. Machine learning in agriculture: A comprehensive updated review. Sensors. 2021;21(11):3758. https://doi.org/10.3390/s21113758
9. Fuentes-Peñailillo F, Gutter K, Vega R, Silva GC. Transformative technologies in digital agriculture: Leveraging Internet of Things, remote sensing and artificial intelligence for smart crop management. J Sens Actuator Netw. 2024;13(4):39. https://doi.org/10.3390/jsan13040039
10. De França e Silva NR, Chaves ME, Luciano AC, Sanches ID, de Almeida CM, Adami M. Sugarcane yield estimation using satellite remote sensing data in empirical or mechanistic modeling: A systematic review. Remote Sens. 2024;16(5):863. https://doi.org/10.3390/rs16050863
11. Da Silva Morales Ú, Rotta MA, Fornari DC, Streit Jr DP. Aquaculture sustainability assessed by emergy synthesis: The importance of

water accounting. Agriculture. 2022;12(11):1947. https://doi.org/10.3390/agriculture12111947

12. Alam SM, Naqvi SS, Ansari RA. Impact of soil pH on nutrient uptake by crop plants. Handbook of plant and crop stress. 1999 May 19;2:51-60.
13. Turner NC. Techniques and experimental approaches for the measurement of plant water status. Plant Soil. 1981;58:339–66. https://doi.org/10.1007/BF02180062
14. Marschner H. Marschner's mineral nutrition of higher plants. 3rd ed. London: Academic Press; 2012. 651 p.
15. Hillel D. Soil and water: physical principles and processes. New York: Academic Press; 1971
16. Richards LA. Diagnosis and improvement of saline and alkali soils. Washington (DC): US Department of Agriculture; 1954. Agricultural Handbook No. 60. p. 7–53.
17. Abrol IP, Yadav JSP, Massoud FI. Salt-affected soils and their management. Rome: Food and Agriculture Organization of the United Nations; 1988. Report No.: FAO Soils Bulletin 39.
18. Khan A, Khan AA, Samreen S, Irfan M. Assessment of sodium chloride (NaCl) induced salinity on the growth and yield parameters of *Cichorium intybus* L. Nat Environ Pollut Technol. 2023;22(2):845-852. https://doi.org/10.46488/NEPT.2023.v22i02.026
19. Savva AP, Frenken K. Irrigation manual: planning, development, monitoring and evaluation of irrigated agriculture with farmer participation. Vol. II, Module 7 [Internet]. Harare: Food and Agriculture Organization of the United Nations, Sub-Regional Office for East and Southern Africa; 2002 [accessed on 2025 Jan 1]. Available from: https://www.fao.org/4/ai596e/ai596e.pdf.
20. Qureshi AS, McCornick PG, Qadir M, Aslam Z. Managing salinity and waterlogging in the Indus Basin of Pakistan. Agric Water Manag. 2008;95(1):1–10. https://doi.org/10.1016/j.agwat.2007.09.014
21. Savci S. Investigation of effect of chemical fertilizers on environment. APCBEE Procedia. 2012;1:287–92. https://doi.org/10.1016/j.apcbee.2012.03.047
22. Ghassemi F, Jakeman AJ, Nix HA. Salinization of land and water resources: human causes, extent, management and case studies. Sydney: University of New South Wales Press; 1995..
23. Global Soil Partnership, Sustainable soil management highlights [Internet]. Food and Agriculture Organization of the United Nations.2021 [cited 2025 Jan 1]. Available from: https://www.fao.org/global-soil-partnership/resources/highlights/detail/en/c/1445579/.
24. NOAA National Centers for Environmental Information. Monthly global drought narrative for October 2024 [Internet]. Published November 2024 [cited 2025 Apr 14]. Available from: https://www.ncei.noaa.gov/access/monitoring/monthly-report/global-drought/202410.
25. Baghour M, Moreno DA, Víllora G, López-Cantarero I, Hernández J, Castilla N, et al. Root-zone temperature influences the distribution of Cu and Zn in potato-plant organs. J Agric Food Chem. 2002;50(1):140-6. https://doi.org/10.1021/jf010375j
26. Baghour M, Ben Chekroun K, Manuel Ruiz Sáez J, Romero L. Root-zone temperature affects the phytoextraction of iron in contaminated soil. J Plant Nutr. 2016;39(1):51-8. https://doi.org/10.1080/01904167.2015.1009105
27. Hussain S, Wang J, Asad Naseer M, Saqib M, Siddiqui MH, Ihsan F, et al. Water stress memory in wheat/maize intercropping regulated photosynthetic and antioxidative responses under rainfed conditions. Sci Rep. 2023;13:13688. https://doi.org/10.1038/s41598-023-40644-1
28. Paut R, Sabatier R, Tchamitchian M. Reducing risk through crop diversification: An application of portfolio theory to diversified horticultural systems. Agric Syst. 2019;168:123-30. https://doi.org/10.1016/j.agsy.2018.11.002
29. Sun B, Gao Y, Yang H, Zhang W, Li Z. Performance of alfalfa rather than maize stimulates system phosphorus uptake and overyielding of maize/alfalfa intercropping via changes in soil water balance and root morphology and distribution in a light chernozemic soil. Plant Soil. 2019;439:145–61. https://doi.org/10.1007/s11104-018-3888-y
30. Wu J, Bao X, Zhang J, Lu B, Sun N, Wang Y, et al. Facilitation between intercropped species increases micronutrient acquisition and controls rust disease on maize. Field Crops Res. 2024;307:109241. https://doi.org/10.1016/j.fcr.2023.109241
31. Li L, Zhang L, Zhang F. Crop mixtures and the mechanisms of overyielding. In: Levin SA, editor. Encyclopedia of biodiversity. 2nd ed. Academic Press; 2013. p. 382–95. https://doi.org/10.1016/B978-0-12-384719-5.00363-4
32. Bargaz A, Noyce GL, Fulthorpe R, Carlsson G, Furze JR, Jensen ES, et al. Species interactions enhance resilience against abiotic stress.Appl Soil Ecol.2017;120:179-188. https://doi.org/10.1016/j.apsoil.2017.08.011
33. Li X, Song Z, Hu Y, Qiao J, Chen Y, Wang S, et al. Drought intensity and post-drought precipitation determine vegetation recovery in a desert steppe in Inner Mongolia, China. Sci Total Environ. 2024;906:167449. https://doi.org/10.1016/j.scitotenv.2023.167449
34. Meißner A, Granzow S, Wemheuer F, Pfeiffer B. The cropping system matters – Contrasting responses of winter faba bean (Vicia faba L.) genotypes to drought stress. J Plant Physiol. 2021;263:153463. https://doi.org/10.1016/j.jplph.2021.153463
35. Renwick LLR, Kimaro AA, Hafner JM, Rosenstock TS, Gaudin ACM. Maize-pigeonpea intercropping outperforms monocultures under drought. Front Sustain Food Syst. 2020;4:562663. https://doi.org/10.3389/fsufs.2020.562663
36. Yin W, Chai Q, Zhao C, Yu A, Fan Z, Hu F, et al. Water utilization in intercropping: A review. Agric Water Manag. 2020;241:106335. https://doi.org/10.1016/j.agwat.2020.106335
37. Ai P, Ma Y, Hai Y. Influence of jujube/cotton intercropping on soil temperature and crop evapotranspiration in an arid area. Agric Water Manag. 2021;256:107118. https://doi.org/10.1016/j.agwat.2021.107118
38. Ghosh PK, Mohanty M, Bandyopadhyay KK, Painuli DK, Misra AK. Growth, competition, yield advantage and economics in soybean/pigeonpea intercropping system in semi-arid tropics of India: I. Effect of subsoiling. Field Crops Res. 2006;96(1):80-89. https://doi.org/10.1016/j.fcr.2005.05.009
39. Caviglia OP, Sadras VO, Andrade FH. Yield and quality of wheat and soybean in sole- and double-cropping. Agron J. 2011;103(4):1081–1089. https://doi.org/10.2134/agronj2011.0019
40. Mu L, Su K, Zhou T, Yang H. Yield performance, land and water use, economic profit of irrigated spring wheat/alfalfa intercropping in the inland arid area of northwestern China. Field Crops Res. 2023;303:109-116. https://doi.org/10.1016/j.fcr.2023.109116
41. Wu K, Fullen MA, An T, Fan Z, Zhou F, Xue G, et al. Above- and below-ground interspecific interaction in intercropped maize and potato: A field study using the 'target' technique. Field Crops Res. 2012;139:63-70. https://doi.org/10.1016/j.fcr.2012.10.002
42. Zancarini A, Lépinay C, Burstin J, Duc G, Lemanceau P, Moreau D, et al. Combining molecular microbial ecology with ecophysiology and plant genetics for a better understanding of plant–microbial communities' interactions in the rhizosphere. In: de Bruijn FJ, editor. Molecular microbial ecology of the rhizosphere. Vol. 1 & 2. Hoboken (NJ): Wiley Blackwell; 2013. p. 69–86. https://doi.org/10.1002/9781118297674.ch7
43. Baghour M, Akodad M, Dariouche A, Maach M, El Haddaji H, Moumen A, et al. Gibberellic Acid and Indole Acetic Acid Improves

Salt Tolerance in Transgenic Tomato Plants Overexpressing LeNHX4 Antiporter. Gesunde Pflanzen. 2023;75:687–693. https://doi.org/10.1007/s10343-022-00734-y

44. Kresnatita S, Ariffin H, Hariyono D, Sitawati. A cauliflower-sweet corn intercropping system in high-temperature conditions. Rev Chapingo Ser Hortic. 2020;26(1):15-27. https://doi.org/10.5154/r.rchsh.2019.09.014

45. Assadi NM, Bijanzadeh E. Influence of relay intercropping of barley with chickpea on biochemical characteristics and yield under water stress. PLOS ONE. 2023;18(6):e0273272. https://doi.org/10.1371/journal.pone.0273272

46. Guo Z, Luo C, Dong Y, Dong K, Zhu J, Ma L. Effect of nitrogen regulation on the epidemic characteristics of intercropping faba bean rust disease primarily depends on the canopy microclimate and nitrogen nutrition. Field Crops Res. 2021;274:108339. https://doi.org/10.1016/j.fcr.2021.108339

47. Zhou Z. Influence of intercropping on soil temperature and crop yield: A study in Jujube-Cotton intercropping systems. Agric Syst. 2022;18(3):1100-1109. https://doi.org/10.7717/peerj.17587/supp-2

48. Lv Q, Chi B, He N, Zhang D, Dai J, Zhang Y, et al. Cotton-Based Rotation, Intercropping and Alternate Intercropping Increase Yields by Improving Root–Shoot Relations. Agronomy. 2023;13(2):413. https://doi.org/10.3390/agronomy13020413

49. Maitra S, Hossain A, Brestic M, Skalicky M, Ondrisik P, Gitari H, et al. Intercropping-A low input agricultural strategy for food and environmental security. Agronomy. 2021;11(2):343. https://doi.org/10.3390/agronomy11020343

50. Zafaranieh M, Valizadeh J. Investigating light absorption and some canopy properties in monocultures and intercropping culture of safflower and chickpea. Int J Agric Innov Res. 2015;3(4):1182-1187. https://doi.org/10.5555/20153142234

51. Li S, Zhao J, Li J, Shao R, Li H, Fang W, et al. Inter- and mixed cropping of different varieties improves high-temperature tolerance during flowering of summer maize. Sustainability. 2022;14:6993. https://doi.org/10.3390/su14126993

52. Liu SB, Chai Q, Huang GB. Relationships among soil respiration, soil temperature and dry matter accumulation for wheat-maize intercropping in an arid environment. Can J Plant Sci. 2013;93(4):715-724. https://doi.org/10.4141/cjps2012-274

53. Ghani MI, Ali A, Atif MJ, Ali M, Amin B, Anees M, et al. Soil amendment with raw garlic stalk: A novel strategy to stimulate growth and the antioxidative defense system in monocropped eggplant in the north of China. Agronomy. 2019;9(2):89. https://doi.org/10.3390/agronomy9020089

54. Wang M, Wu C, Cheng Z, Meng H. Growth and physiological changes in continuously cropped eggplant (Solanum melongena L.) upon relay intercropping with garlic (Allium sativum L.). Front Plant Sci. 2015;6:262. https://doi.org/10.3389/fpls.2015.00262

55. Ahmad S, Ghafoor A, Akhtar ME, Khan MZ. Implication of gypsum rates to optimize hydraulic conductivity for variable-texture saline-sodic soils reclamation. Land Degrad Dev. 2016;27(3):550-560. http://dx.doi.org/10.1002/ldr.2413

56. Singh YP, Mishra VK, Sharma DK, Singh G, Arora S, Dixit H, et al. Harnessing productivity potential and rehabilitation of degraded sodic lands through jatropha-based intercropping sequences. Agric Ecosyst Environ. 2016;233:121–129. https://doi.org/10.3389/fpls.2015.00262

57. Jurado C, Díaz-Vivancos P, Gregorio BE, Acosta-Motos JR, Hernández JA. Effect of halophyte-based management in physiological and biochemical responses of tomato plants under moderately saline greenhouse conditions. Plant Physiol Biochem. 2024;206:108-228. https://doi.org/10.1016/j.plaphy.2023.108228

58. Ahmad R, Zaheer SH. Responses of Sporobolus arabicus and Sesbania aegyptica as affected by density, salinity of irrigation water and intercropping. Pak J Bot. 1994;26:115. https://doi.org/10.5555/19950709605

59. Shi X, Guo P, Ren J, Zhang H, Dong Q, Zhao X, et al. A salt stress tolerance effect study in peanut based on peanut/sorghum intercropping system. Sci Agric Sin. 2022;55:2927–2937. https://doi.org/10.3864/j.issn.0578-1752.2022.15.005

60. Guo T, Yao X, Wu K, Guo A, Yao Y. Response of the rhizosphere soil microbial diversity to different nitrogen and phosphorus application rates in a hulless barley and pea mixed-cropping system. Appl Soil Ecol.2024;195:105262 https://doi.org/10.1016/j.apsoil.2023.105262

61. Arora P, Bidalia A, Rao KS. Growth and photosynthetic response of wheat and mustard plants to intercropping. Phytomorphology. 2016;66:35-44.

62. Slatni T, Selmi A, Kalboussi N, Zemni H, Echadly A, Espin GB, et al. Intercropping salt-sensitive *Solanum lycopersicum* L. and salt-tolerant Arthrocaulon macrostachyum in salt-affected agricultural soil under open field conditions: physiological, hormonal, metabolic and agronomic responses. Environ Exp Bot. 2024;228:106013. https://doi.org/10.1016/j.envexpbot.2024.106013

63. Wang S, Liu J, Liu Y, Tian C. Enhanced soybean growth and the associated ion balance, nutrient accumulation and rhizosphere bacterial community when intercropped with Suaeda salsa in saline soils. Agronomy. 2024;14(10):2181. https://doi.org/10.3390/agronomy14102181

64. Atzori G, Guidi Nissim W, Mancuso S, Palm E. Intercropping salt-sensitive *Lactuca sativa* L. and salt-tolerant *Salsola soda* L. in a saline hydroponic medium: an agronomic and physiological assessment. Plants. 2022;11(21):2924. https://doi.org/10.3390/plants11212924

65. Ghaffarian MR, Yadavi A, Movahhedi Dehnavi M, Dabbagh Mohammadi Nassab A, Salehi M. Improvement of physiological indices and biological yield by intercropping of Kochia (Kochia scoparia), Sesbania (Sesbania aculeata) and Guar (Cyamopsis tetragonoliba) under the salinity stress of irrigation water. Physiol Mol Biol Plants. 2020;26:1319-1330. https://doi.org/10.1007/s12298-020-00833-y

66. Sekar J, Saharan K, Raju K, Singh U, Vaiyapuri PR. Consequences of bioinoculants and intercropping approach to alleviate plant drought and salinity stress for sustainable agriculture. In: Akhtar M, editor. Salt stress, microbes and plant interactions: mechanisms and molecular approaches. Singapore: Springer; 2019. p. 161–82. https://doi.org/10.1007/978-981-13-8805-7_8

67. Simon NS, Mmateko KP, Bob OJ. Maize-legume intercropping system improved soil quality under irrigated and rainfed conditions. Res Crops. 2024;25(4):553-559. https://doi.org/10.31830/2348-7542.2024.ROC-1117

68. Wang S, Ge S, Mai W, Tian C. Nitrogen promotes the salt-gathering capacity of Suaeda salsa and alleviates nutrient competition in the intercropping of Suaeda salsa/Zea mays L. Int J Mol Sci. 2022;23(24):15495. https://doi.org/10.3390/ijms232415495

69. Shi X, Zhou Y, Guo P, Ren J, Zhang H, Dong Q, et al. Peanut/sorghum intercropping drives specific variation in peanut rhizosphere soil properties and microbiomes under salt stress. Land Degrad Dev. 2023;34(3):736-750. https://doi.org/10.1002/ldr.4490

70. Simpson CR, Franco JG, King SR, Volder A. Intercropping halophytes to mitigate salinity stress in watermelon. Sustainability. 2018;10(3):681. https://doi.org/10.3390/su10030681

71. Castagna A, Mariottini G, Gabriele M, Longo V, Souid A, Dauvergne X, et al. Nutritional composition and bioactivity of Salicornia europaea L. plants grown in monoculture or intercropped with tomato plants in salt-affected soils. Horticulturae. 2022;8(9):828. https://doi.org/10.3390/horticulturae8090828

72. Jurado-Mañogil C, Barbara-Espin G, Hernández JA, Díaz-Vivancos

P. Comparative metabolomic analysis between tomato and halophyte plants under intercropping conditions. Physiol Plant. 2023;175(4):e13971. https://doi.org/10.1111/ppl.13971

73. Shi X, Zhou Y, Zhao X, Guo P, Ren J, Zhang H, et al. Soil metagenome and metabolome of peanut intercropped with sorghum reveal a prominent role of carbohydrate metabolism in salt-stress response. Environ Exp Bot. 2023;209:105274. https://doi.org/10.1016/j.envexpbot.2023.105274

74. Chai Q, Nemecek T, Liang C, Zhao C, Yu A, Coulter JA, et al. Integrated farming with intercropping increases food production while reducing environmental footprint. Proc Natl Acad Sci USA. 2021;118(38):e2106382118. https://doi.org/10.1073/pnas.2106382118

75. Wang W, Chen Y, Zhang F, Zhang W, Liu J, Wang J, et al. Cotton-maize intercropping increases rhizosphere soil phosphorus bioavailability by regulating key phosphorus cycling genes in northwest China. Appl Soil Ecol. 2023;182:104734. https://doi.org/10.1016/j.apsoil.2022.104734

76. Ngwene B, Neugart S, Baldermann S, Ravi B, Schreiner M. Intercropping induces changes in specific secondary metabolite concentration in Ethiopian kale (Brassica carinata) and African nightshade (Solanum scabrum) under controlled conditions. Front Plant Sci. 2017;8:1700. https://doi.org/10.3389/fpls.2017.01700

77. Inal A, Gunes A. Interspecific root interactions and rhizosphere effects on salt ions and nutrient uptake between mixed-grown peanut/maize and peanut/barley in original saline-sodic-boron toxic soil. J Plant Physiol. 2008;165(5):490–503. https://doi.org/10.1016/j.jplph.2007.01.016

78. Guo X, Xiong H, Shen H, Qiu W, Ji C, Zhang Z, et al. Dynamics in the rhizosphere and iron-uptake gene expression in peanut induced by intercropping with maize: role in improving iron nutrition in peanut. Plant Physiol Biochem. 2014;76:36–43. https://doi.org/10.1016/j.plaphy.2013.12.019

79. Dai J, Qiu W, Wang N, Nakanishi H, Zuo Y. Comparative transcriptomic analysis of the roots of intercropped peanut and maize reveals novel insights into peanut iron nutrition. Plant Physiol Biochem. 2018;127:516–524. https://doi.org/10.1016/j.plaphy.2018.04.024

80. Zhou Q, Chen J, Xing Y, et al. Influence of intercropping Chinese milk vetch on the soil microbial community in the rhizosphere of rape. Plant Soil. 2019;440:85–96. https://doi.org/10.1007/s11104-019-04040-x

81. Zheng Y, Zhang F, Li L. Iron availability as affected by soil moisture in intercropped peanut and maize. J Plant Nutr. 2003;26:2425-2437. https://doi.org/10.1081/PLN-120025470

82. Chi B, Liu J, Dai J, Li Z, Zhang D, Xu S, et al. Alternate intercropping of cotton and peanut increases productivity by increasing canopy photosynthesis and nutrient uptake under the influence of rhizobacteria. Field Crops Res. 2023;302:109059. https://doi.org/10.1016/j.fcr.2023.109059

83. Jensen ES, Carlsson G, Hauggaard-Nielsen H. Intercropping of grain legumes and cereals improves the use of soil N resources and reduces the requirement for synthetic fertilizer N: a global-scale analysis. Agron Sustain Dev. 2020;40:5. https://doi.org/10.1007/s13593-020-0607-x

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.