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Plant diversity as a sustainable strategy for mitigating biotic and abiotic stresses in tomato cultivation

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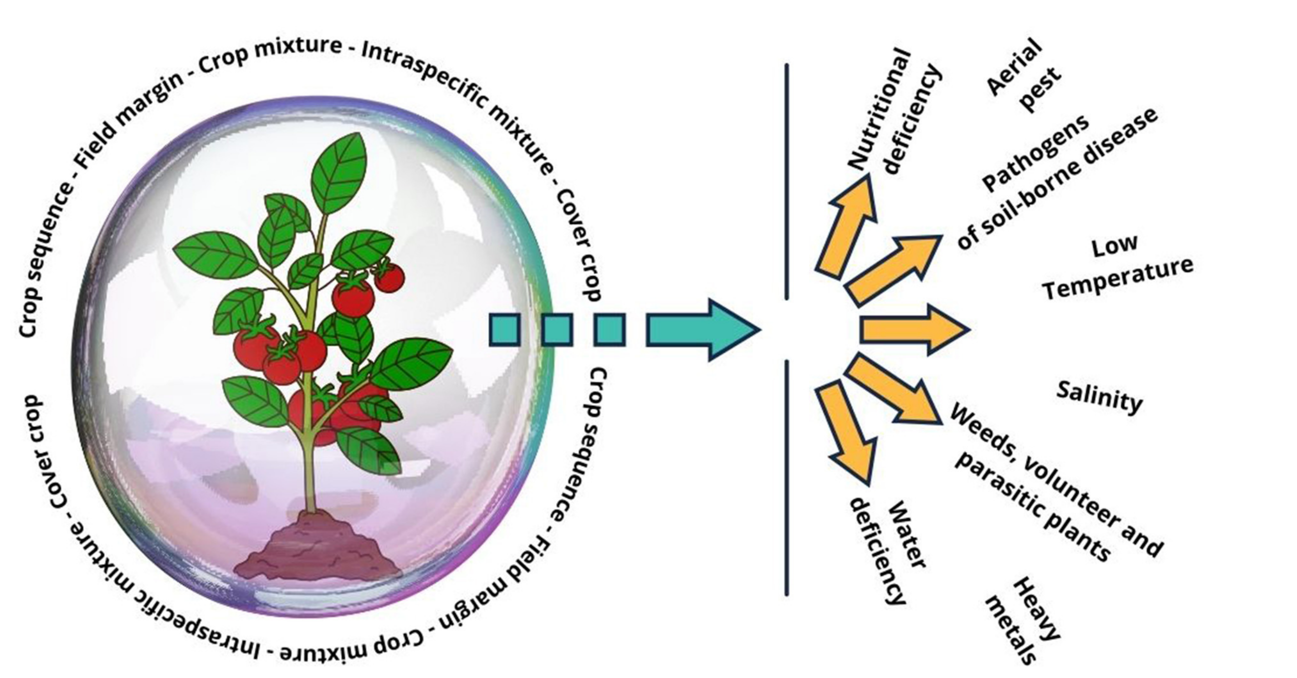
Sustainable agriculture has become a global priority in response to increasing food demand and the challenges confronting agricultural production, such as biotic and abiotic stresses. In this review, we delve into the role of plant diversity in mitigating these stressors within tomato cultivation. Our investigation reveals that the most extensively studied companion species are *Vicia villosa* Roth, *Coriandrum sativum* L., and *Allium cepa* L., while the primary stressors under scrutiny include nutrient deficiencies, aerial pests, and soil-borne pathogenic diseases. Regarding nutrient deficiencies, the cover crop system has demonstrated its capacity to provide essential nutrients directly and indirectly to plants. In addressing aerial pests and pathogens, all cultivation systems exhibit contributions. Finally, we assert that incorporating plant diversity into agroecosystems can effectively counteract various types of stressors. These benefits align with the application of agroecological principles and the development of sustainable agroecosystems. Further assessments of the effects of additional companion plant species are imperative. This should encompass the identification of their distribution, optimal plant quantities, and cultivation systems that enhance their benefits. Ultimately, these evaluations will aid in the formulation of comprehensive guidelines to facilitate the selection and utilization of plant diversity for long-term sustainability.

KEYWORDS

agrobiodiversity, agricultural diversification, agroecology, green manures, plant diversity, integrated pest management

1 Introduction

Agriculture, one of the foundational pillars of human civilization, confronts unparalleled challenges in the twenty first century (Wilson and Lovell, 2016; Sumberg and Giller, 2022). The achievement of successful food production hinges significantly on the growth and development of plants, a process intricately connected to the presence of stress, whether of biotic or abiotic origins (Enebe and Babalola, 2018).



GRAPHICAL ABSTRACT

Abiotic stress, encompassing salinity, drought, extreme temperatures, and exposure to toxic metals, in conjunction with biotic stress arising from attacks by herbivorous insects and pathogens, presents a determining factor in crop productivity (Benavidez et al., 2002; Song et al., 2015; Zhu, 2016; Inbaraj, 2021). In recent decades, climate change and pollution of water and soil have led to stress conditions appearing more frequently in crops (Volpe et al., 2018; Nawaz et al., 2020; Peck and Mittler, 2020); these factors are also closely related to intensive agricultural practices like continuous monoculture and the excessive application of fertilizers and pesticides (Corrado et al., 2019).

In this critical context, the imperative for an extensive review becomes evident—not only to illuminate how stress impacts crops but also to explore strategies for mitigating its effects. From an agroecological standpoint, conserving biodiversity within agroecosystems has evolved into a foundational principle for alleviating the stresses impacting agricultural production (Wezel et al., 2020). This global diversity encompasses a wide range of plants, animals, and microorganisms chosen for agriculture, as well as the associated wild biodiversity (Wood et al., 2015). As the scientific and agricultural communities increasingly acknowledge the potential of deliberate and associated agrobiodiversity, an invaluable approach known as functional diversity is emerging. Functional diversity, which considers trophic interactions and the functional traits of species, emerges as a promising approach to understanding how agrobiodiversity can effectively counteract the impacts of stress (Calow, 1987; Wood et al., 2015). In this regard, agricultural diversification is the intentional addition of functional biodiversity through different cropping systems at multiple spatial and/or temporal scales (Kremen et al., 2012; Gaba et al., 2015; Tamburini et al., 2020). This review aims to analyze the reported benefits over the last 10 years of agricultural diversification in mitigating different types of biotic and abiotic stresses in tomato (*Solanum lycopersicum* L), which, due to its status as a high-yielding crop, high economic value, its rich dose of nutrients such as lycopene and carotenoids, as well as its versatility in cooking, is the most produced vegetable in the world and an important food component of the daily diet in most countries (Anwar et al., 2019). A comprehensive review was conducted by consulting two leading academic databases, SCOPUS and Web of Science (WOS), of research articles on tomatoes grown in one of the cropping systems proposed by Gaba et al. (2015): intercropping, crop sequence, field margin, and cover crop.

2 Abiotic stress

Climate change and pollution of water and soil have led to stress conditions such as drought, chilling, water deficits, and heavy metal presence appearing more frequently in crops (Nawaz et al., 2020; Hasan et al., 2023; Raza et al., 2023; Singh et al., 2023). Utilizing plant companions within different crop systems has demonstrated the ability to mitigate various abiotic stresses; notably, soil nutrient deficiency represents the most extensively studied abiotic stress type (Table 1).

2.1 Soil nutrient deficiency

Soil nutrient deficiency refers to the lack or insufficiency of essential nutrients for proper plant growth and development in a specific soil area (Roy et al., 2006). Soil nutrients, such as nitrogen, phosphorus, potassium, calcium, magnesium, and various micronutrients, are essential for plant growth

TABLE 1 The advantages of companion species in various crop systems for mitigating different abiotic stresses.

Companion species	Crop system	Infrastructure	Benefit	References
Low temperature				
Wheat (*Triticum aestivum* L.)	Intercropping	-	Mitigates the negative impact of winter climate conditions on tomato flowering, fruit set, and productivity	Sheha et al., 2022
Heavy metals				
Sweet pepper (*Capsicum annuum* L.-cv. Cleor); zucchini (*Cucurbita pepo* L.-cv. Primula); Hairy vetch (*Vicia villosa* Roth)	Cover crop; intercropping	-	Cover crops reduce the accumulation of As in the roots, stems, leaves, and total biomass of tomato, sweet pepper, and zucchini	Mancinelli et al., 2019
Eclipta prostrata L.; *Crassocephalum crepidioides* Benth.		-	Inter-cropping with three plant species resulted in maximum root and shoot biomasses for tomato seedlings and reduced Cd content in tomato seedlings to a minimum	Xie et al., 2021
Nutrient deficit				
Barley (*Hordeum vulgare* L.); hairy vetch (*V. villosa*)	Cover crop	-	Pure vetch provided optimal N status for the following crop but led to increased nitrate leaching. Mixture of 75% vetch and 25% barley ensured an adequate N supply for tomatoes while reducing the concentration of NO_3-N in the soil solution	Farneselli et al., 2018
		-	Cultivating pure barley or a barley-vetch mixture (with a higher proportion of barley) reduced N leaching but had variable effects on N uptake by tomatoes. This suggests the necessity for adaptable N supplementation to achieve optimal tomato N nutrition and maximize fruit yield	Farneselli et al., 2020
Cowpea (*Vigna unguiculata* L.)	Cover crop	Greenhouse	The combination of cover crops and farmyard manure increases both total N levels and nitrate concentrations in the soil, leading to higher fruit yields in tomato crops	Gatsios et al., 2019
Hairy vetch (*V. villosa*)	Cover crop	Plastic high tunnel	The use of cover crops increased soil carbon and N stocks and resulted in the highest soil N availability and greater N uptake	Muchanga et al., 2019
		Greenhouse	Although the cover crop had a limited short-term nitrogen-supplying effect, it could also function as a long-term nitrogen source, lasting for up to two cycles after the cover crop is used	Sugihara et al., 2016
		-	The nitrogen obtained from the cover crop was efficiently absorbed with a minimal amount of chemical fertilizers, making it a viable alternative nitrogen fertilizer source	Sugihara et al., 2013
		-	The cover crop served as a quick-release fertilizer	Sugihara et al., 2014
Hairy vetch (*V. villosa*); rye (*Secale cereale* L.)	Cover crop	-	The mixture of 67% vetch and 33% rye increased the total N content in the topsoil and resulted in higher tomato yields, with minimal residual N	Muchanga et al., 2020b
		Plastic high tunnel	A combination of cover crops can release significant amounts of N during both the early and late stages of tomato cultivation	Muchanga et al., 2020a
Oat (*Avena sativa* L.); oilseed radish (*Raphanus sativus* L.); winter cereal rye (*S. cereale*)	Cover crop	-	Cover crops did not reduce the mineral N content in the soil during the fall season and increased tomato yield. Among all the cover crop species, radish accumulated the highest amount of N in its above-ground parts during the fall	Chahal and Van Eerd, 2021
Oat (*A. sativa*); oilseed radish (*R. sativus*); hairy vetch (*V. villosa*); clover (*Trifolium vesiculosum* Savi.)	Cover crop	-	The use of radish cover crops increased soil P, Ca, and K levels. This increase in nutrient availability could be one of the factors contributing to the overall increase in total crop production	Galvão et al., 2013
Oilseed radish (*R. sativus*)	Cover crop	-	The cover crop increases soil mineral N levels during its growth and continues to do so into the tomato growing season	Belfry et al., 2017
Pea (*Pisum arvense* L.); barley (*H. vulgare*)	Cover crop	-	The mixture of 25% barley and 75% pea increases N recycling, regardless of the soil management strategy (no-till or conventional tillage)	Tosti et al., 2019

(Continued)

TABLE 1 (Continued)

Companion species	Crop system	Infrastructure	Benefit	References
Sunn hemp (*Crotalaria junceae* L.); millet (*Pennisetum americanum* L.)	Cover crop	-	No-tillage following cover crops (both millet and sunn hemp) reduces the N requirements while achieving high tomato production	Branco et al., 2017
Faba bean (*Vicia faba* L.); wheat (*T. aestivum*); oilseed radish (*R. sativus*)	Cover crop	-	*V. faba* enhanced the effects of externally input N	Fracchiolla et al., 2021
Lettuce (*Lactuca sativa* L. var. Romana, var. Tantan, var. capitata)	Cover crop; crop sequence	High tunnel	Cover crops played a crucial role in preserving plant-available N within organic matter and increasing the availability of Ca, Mg, K, and P. N uptake by the subsequent cash crop was higher in pea monoculture compared to the pea-oat mixture and when used as green manure rather than mulch	Domagała-Swiatkiewicz and Siwek, 2022
Maize (*Zea mays* L.); alfalfa (*Medicago sativa* L.)	Crop sequence	-	Incorporating legumes into a tomato-maize rotation reduced the presence of genes associated with denitrification and facilitated the colonization of various bacterial and fungal groups capable of enhancing soil nutrient availability	Samaddar et al., 2021
		-	Continuous cultivation with alfalfa as a perennial crop effectively reduced NO_3-leaching	Woodward et al., 2022
Celery; lettuce; clover	Crop sequence; cover crop	Greenhouse	Incorporating legumes into vegetable crop rotations reduced N input by 25%	Min et al., 2016
Potato onion (*Allium cepa* L.)	Intercropping	Greenhouse	Intercropping increased the abundance of P-solubilizing microbial communities when exposed to all tested P forms, including Al-P, Fe-P, Ca-P, and O-P	Khashi u Rahman et al., 2021
		Greenhouse	Interspecific interactions led to increased growth and P concentration in tomatoes, especially in the absence of P fertilization. However, these interactions harmed the growth of potato-onion plants	Gao et al., 2021b
		Greenhouse	Intercropping enhanced the growth and P uptake of tomato seedlings, but it decreased the growth and P uptake of potato onion plants	Wu et al., 2016
		Greenhouse	Intercropping with biochar improved soil physicochemical conditions, enhanced plant nutrient uptake, and influenced soil microbial communities	He et al., 2021
		Greenhouse	Intercropping increased the percentage of root length colonized by hyphae and arbuscules, as well as K content in tomatoes, but decreased these factors in potato-onions	Gao et al., 2021a
Faba bean (*V. faba*)	Intercropping; crop sequence	-	Strip cropping increases P uptake. The N inputs from faba beans can potentially provide sufficient N to support tomato production, but these inputs can vary significantly. Therefore, quick estimates are necessary to determine the need for additional fertilization	Warren-Raffa et al., 2022
Veza villosa (*V. villosa*)	Cover crop	-	Tomato plants grown with vetch showed reduced effects of N toxicity and maintained high photosynthetic rates even with high levels of inorganic nitrogen	Fatima et al., 2012
Salinity				
Cereal	Crop sequence	-	Introducing fallow cereal immediately after tomatoes or peppers in the rotation leads to a reduction in soil salinity of ∼56% (∼2 dS/m)	Bani et al., 2021
Salsola soda L.	Intercropping	Greenhouse	Combining *S. soda* with tomato cultivation in highly saline soils ensure both yield and quality of tomatoes	Karakas et al., 2016
Arthrocaulon macrostachyum L.	Intercropping; crop sequence	Greenhouse	Both intercropping and sequential cropping decreased chloride content, sodium adsorption ratio, and electrical conductivity, leading to reduced soil salinity	Jurado et al., 2024
Water deficiency				
Velvet bean (*Mucuna pruriens* L.); Tanzanian sunhemp (*Crotalaria ochroleuca* G. Don.); purple vetch (*Vicia benghalensis* L.)	Cover crop	-	The inclusion of cover crops improves soil moisture retention, leading to higher tomato yields and enhanced water utilization efficiency. Moreover, when vetch biomass is integrated into the soil, both above and below ground, it increases the amount and frequency of deep percolation	Karuku et al., 2014

(Continued)

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TABLE 1 (Continued)

Companion species	Crop system	Infrastructure	Benefit	References
Brown mustard (*Brassica juncea* L.); wheat (*T. aestivum*); green beans (*Phaseolus vulgaris* L.)	Crop sequence	-	The rotation of tomato, bean, wheat, and mustard enhances N-mineralization, resulting in reduced fertilizer and irrigation inputs compared to other rotation schemes	Kayikcioglu et al., 2020
Maize (Zea mays L.)	Intercropping	-	Tomato yields of up to 32 ton ha $^{-1}$ can be obtained in rainfed conditions when local tomato cultivars adapted to hot and dry climatic conditions are intercropped with corn	Castronuovo et al., 2023

(Kathpalia and Bhatla, 2018). Their absence or low availability can limit plant health and have a negative impact on crop quality and yield (Tripathi et al., 2022). Particularly, tomatoes are a crop known for requiring high nutrient inputs because of their extensive vegetative biomass production, heavy fruit load, and long growing season (Neocleous et al., 2021). Used biodiversity can enhance nutrient supply and assimilation, primarily through cover crops; also known as green manures, when a legume is used (Farneselli et al., 2018). A widely used green manure is hairy vetch (*V. villosa*), which can contribute optimal nitrogen levels to the tomato crop as a fast-release fertilizer, facilitating nitrogen uptake by up to 38% (Sugihara et al., 2013; Muchanga et al., 2019). However, the fast-release of hairy vetch does not prevent N leaching unless used in mixtures with cereals such as barley (*Hordeum vulgare* L.) or rye (*Secale cereale* L.); these mixtures increase the carbon/nitrogen ratio, which slow the rate of nitrogen (N) release and favors the retention of up to 47.0% of the nitrogen produced, thus mitigating this problem (Tosti et al., 2014; Farneselli et al., 2020; Muchanga et al., 2020a).

Although cover crops have been shown to supply considerable N, they are typically used in combination with synthetic fertilizers because the N supply of cover crops is unpredictable and variable and not always synchronized with the needs of the tomato plant (Farneselli et al., 2020). However, green manure may act as an alternative N fertilizer, which enhances the efficiency of external nitrogen inputs and can reduce their requirements. For example, the use of hairy vetch, showed a reduction in external nitrogen inputs by at least 50–66%, primarily during the 4 weeks after transplant when N uptake derived from hairy vetch is higher (Sugihara et al., 2013). Branco et al. (2017) also observed that the use of sunn hemp (*Crotalaria junceae* L.) and millet (*Pennisetum americanum* L.) as green manures enhanced the efficiency of external nitrogen inputs, which reduced the requirement of external nitrogen input. Acording Yang et al. (2023), the combination of organic and inorganic fertilizers, also have a significant positive effect on the fruit weight, number, size, elemental content, total yield, and plant height of the tomato crop.

While nitrogen represents the main nutrient contribution of green manures, Fatima et al. (2012) found that hairy vetch (*V. villosa*), in addition to nitrogen, also provides significant potassium inputs to the tomato crop, as in the case of nitrogen, the potassium content was 125 mg kg^{-1} and nitrogen 23 mg kg^{-1} in soil without hairy vetch, while 173 mg kg^{-1} and 56 mg kg^{-1} was reported in soils with hairy vetch respectively; and Domagała-Swiatkiewicz and Siwek (2022) report that the use of pea (*Pisum sativum* L.) and a mixture of pea and oat (*Avena sativa* L.) as green manure or organic mulch significantly improve the availability of other essential elements, including calcium (Ca), magnesium (Mg), potassium (K) and phosphorus (P) compared to the control.

In addition to cover crops, intercrops such as tomatoes with potato-onion (*A. cepa*) have demonstrated the promotion of a higher abundance of microbial communities capable of solubilizing different forms of phosphorus, which is positively correlated with the availability of this nutrient (Khashi u Rahman et al., 2021).

2.2 Low-temperature

Tomato originating from subtropical regions is notably susceptible to low-temperature stress and suffers injury at temperatures below 13°C (Pandey et al., 2011; Anwar et al., 2019). Cold temperatures lead to issues such as flower abscission, pollen sterility, ovule abortion, and reduced fruit set, ultimately affecting the final yield (Pandey et al., 2011; Albertos et al., 2019).

To safeguard crops against frost, farmers have employed diverse intervention methods, such as wind machines or greenhouse heating, which incur high energy costs and may offer limited protection (Van Ploeg and Heuvelink, 2005; Albertos et al., 2019). In contrast, intercropping emerges as a sustainable alternative to mitigate the effects of cold stress. An illustrative example is the recent study by Sheha et al. (2022), suggesting that intercropping wheat (*Triticum aestivum* L.) with tomatoes could be an effective measure against cold and frost; their results show that a seeding rate of 50% led to a significant 9.4% increase in fruit yield per plant compared to a 25% seeding rate because increasing the wheat seeding rate enhances protection against cold temperatures by trapping warm air closer to the plants and reducing heat loss through soil convection; they also consider as a crucial factor the wheat sowing date, which must allow for tomato plant growth before facing severe competition with wheat for essential growth resources.

2.3 Salinity

Salinization, primarily caused by irrigation and fertilization practices, affects soil quality and productivity (Tomaz et al., 2020; Martínez-Sias et al., 2022; Khasanov et al., 2023). This elevated concentration of salts dissolved in the soil solution has adverse consequences on tomatoes, including slowed or reduced seed germination, decreased nutrient absorption, and restricted plant growth (Ondrasek et al., 2022; Khasanov et al., 2023).

Various solutions have been proposed to combat salinization, including promoting plant diversity (Ondrasek et al., 2022). For example, in open field conditions, after tomato cultivation irrigated with saline groundwater, the soil reaches a salinity of ~6 dS/m, but if tomato cultivation is followed by sequences of three crops, the salinity decreases to ∼1 dS/m; this is possible because, during the rainfed crops period, rain does the leaching process by washing away the salts in the soil; therefore, salinity varies depending on the growing season and rainfall (Bani et al., 2021).

In the greenhouse context, introducing salt-resistant companion plants has proven to be an effective strategy for reducing soil salinity and safeguarding tomato production. For example, the yield of a tomato grown with companion plants of *Salsola soda* L. in soils with high salt content increased from 20.3 g plant^{-1} when the tomato was grown alone to 229.7 g plant^{-1} because *S. soda* absorbs and stores soil salts in its tissues (Karakas et al., 2016). The halophyte Arthrocaulon macrostachyum L., in intercropping and sequential cropping with tomato, also reduced soil salinity under moderately saline conditions and enhanced tomato yield (Jurado et al., 2024).

2.4 Water deficiency

Tomato crops have high water requirements, making scarcity a limiting factor that can cause delays in plant development and reduce the number of fruits in clusters (Alomari-Mheidat et al., 2023). There are few studies on how cover crops can contribute to avoiding the impacts of water deficiencies; however, Schomberg et al. (2023) mention that they offer a promising solution because they can reduce runoff, enhance infiltration and minimize evaporation which favors water storage and soil moisture conservation. In this regard (Karuku et al., 2014), studied how purple vetch (*Vicia benghalensis* L.) as a cover crop improves tomato yield and water use efficiency by 80% and 57% above control, respectively. In addition to cover crops, intercropping local tomato cultivars adapted to hot and dry conditions with corn allows yields of up to 32 ton ha $^{-1}$ under rainfed conditions (Castronuovo et al., 2023).

2.5 Heavy metals toxicity

Heavy metal toxicity is widespread in agricultural soils across the globe (Ur Rahman et al., 2023). The origin and impact of these pollutants on agriculture vary depending on every heavy metal and crop (Selvi et al., 2019; Joshi and Gururani, 2023; Rashid et al., 2023). Agronomic interventions such as phytoremediation using hyper-accumulator plants to remove contaminants from soil and water is one of the effective methods to remove heavy metals (Elango et al., 2022). For instance, low concentrations of arsenic (As) can stimulate tomato growth, but high concentrations inhibit germination, reduce root and shoot development, lower yield, disrupt photosynthesis and mineral nutrition, and induce necrosis (Sandil et al., 2021). To manage this issue, Mancinelli et al. (2019) explored biodiversity; their study revealed that when preceded by *V. villosa* as green manure, tomato crops accumulated lower levels of As in their total biomass and yielded higher crop yields.

Cadmium (Cd) is found naturally in the environment and is also generated through human activities, such as phosphate fertilizers (Rahim et al., 2022). Cadmium toxicity can disturb the uptake and translocation of essential mineral nutrients in plants, affecting plant metabolism and inhibiting growth and development (Qin et al., 2020). However, Xie et al. (2021) investigated the effects of intercropping tomatoes with the accumulator plant *Eclipta prostrata* L. and hyperaccumulator plant *Crassocephalum crepidioides* Benth; their study demonstrated a significant increase in the biomass of tomato seedlings; additionally, Cd contents in the roots and shoots of tomato seedlings decreased by 17.35% and 22.35%, respectively.

3 Biotic stress

The widespread application of pesticides has caused imbalances inside and outside the plots where they are applied (Maurya et al., 2019). For example, they have caused the resistance of many pests to insecticides, affected beneficial organisms such as pollinators, predators, and parasitoids, and damaged non-target organisms several kilometers from the point of their original release (Aktar et al., 2009; Abad et al., 2020). Agricultural diversification offers a viable alternative to reduce the impacts of crop pests and diseases and dependence on pesticides, as well as to control weeds, although in the latter case, there are still few studies, as shown in Table 2.

3.1 Aerial pest

Pests cause 20% of global annual crop losses (Mateos-Fernández et al., 2022). This vulnerability of crops is observed, particularly in monoculture systems (Ratnadass et al., 2021). Incorporating high functional biodiversity through different cropping systems contributes to maintaining ecological functions that help pest management (Altieri et al., 2015). For aerial pests case, intercropping has proven to be particularly effective because companion plants play multiple roles, serving as repellents, reservoirs for natural enemies, and creating visual and olfactory barriers (Togni et al., 2016; Carvalho et al., 2017; Pouët et al., 2022). For example, Mutisya et al. (2016) observed that a row of aromatic basil (*Ocimum basilicum* L.) as companion cropping between adjacent tomato rows significantly lowered whitefly (*Bemisia tabaci* Genn) infestation in tomatoes by 68.7% and resulted in 13.75 t/ha^{-1} as tomato yield compared to 5.9 t/ha^{-1} in the control because attractive nature of the basil plant makes it a better host for insects such as *B. tabaci*. Moreover, the essential oils and volatiles of wild oregano (*Plectranthus amboinicus* Lour.), coriander (*Coriandrum sativum* L.), and Greek basil (*Ocimum minimum* Labiatae) have been shown to repel *B. tabaci* when grown with tomatoes (Carvalho et al., 2017; Pouët et al., 2022); additionally, *C. sativum* shown to reduces the tomato damage caused by *Tuta absoluta* Meyrick and *Spodoptera eridania* Cramer, and attract females of *Cycloneda sanguinea* L. who use coriander plants as oviposition sites and help control aphids of infested tomato plants (Marouelli et al., 2013; Togni et al., 2016). Another companion plant that attracts predators is sesame (*Sesamum indicum* L.), which helps to maintain the zoophytophagus mirid *Nesidiocoris tenuis* Reuter populations during the entire tomato cropping season and reduces up to 75% of the whitefly numbers compared to untreated tomatoes. Management of *B. tabaci* also contributes to reduced disease transmission, such as Begomovirus (Togni et al., 2018).

TABLE 2 Advantages of partner plant species in various crop systems for mitigating diverse biotic stresses.

Companion species	Crop system	Infrastructure	Benefit	References
Aerial pest				
Asteraceae	Crop sequence	Greenhouse	Tomato plants cultivated in soil previously occupied by Asteraceae family plants displayed significant resistance to caterpillar feeding by *Manduca sexta* L.	Ingerslew and Kaplan, 2018
-	Field margin	-	Field margins increase the diversity of natural enemies and decrease damage caused by Lepidoptera pests like *Tuta absoluta* Meyrick. However, total crop damage increases with the expansion of arable land	Balzan et al., 2015
Buckwheat (*Fagopyrum esculentum* Moench.)	Field margin	-	The parasitism rates of *Nezara viridula* L. eggs by *Trissolcus basalis* Wollaston decrease as the distance from the field margin with buckwheat increases	Foti et al., 2019
Sown flower strips; semi-natural margins	Field margin	-	Sown flower strips serve as protective covers against sap-sucking pests, increasing the parasitism rate of aphids, reducing the rate of foliar damage caused by lepidopterans, and enhancing associations with natural enemies. Their effectiveness is further improved when combined with the conservation of diverse seminatural vegetation in the existing field margin	Balzan and Moonen, 2014
Sown mixtures; natural vegetation	Field margin	-	The abundance and diversity of beneficial arthropods were greater in the sown mixture than in natural vegetation	Kati et al., 2021
Basil (*Ocimum basilicum* L.)	Intercropping	-	Companion cropping with a row of basil planted between adjacent tomato plants and covered with Agronet significantly reduced *Bemisia tabaci* Genn. infestation in tomatoes by 68.7%	Mutisya et al., 2016
Coriander (*Coriandrum sativum* L.)	Intercropping	Greenhouse	Coriander volatiles attract *Cycloneda sanguinea* L. adults, and females also use coriander plants as oviposition sites. Larvae hatching on coriander find nearby aphid-infested tomato plants within about 3 days after hatching	Togni et al., 2016
		-	Intercropping reduces the damage caused by *T. absoluta* and *Spodoptera eridania* Cramer in organic production systems	Marouelli et al., 2013
Persian clover (*Trifolium resupinatum* L.)	Intercropping	-	Intercropping reduces the density and increases parasitism rates of *Helicoverpa armigera* Hubner eggs and larvae, especially with row ratios of tomato-clover 1:2 and 2:2. Additionally, the average number of predatory bugs increases with a higher proportion of clover/tomato rows	Abad et al., 2020
Sesame (*Sesamum indicum* L.)	Intercropping	-	*Nesidiocoris tenuis* Reuter are zoophytophagous mirids used successfully as an alternative for controlling *B. tabaci*. However, this control agent can become a pest of tomatoes when prey is scarce. Intercropping helps maintain the populations of *N. tenuis* with minimal damage to tomatoes	Castillo et al., 2022
Solanum lycopersicum var. cerasiforme	Intraspecific mixture	-	Monocropping wild tomatoes and intercropping wild and cultivated tomato plants both result in reduced levels of *T. absoluta* infestation	Miano et al., 2022
Wild oregano (*Plectranthus amboinicus* Lour.)	Intercropping	Greenhouse	In a greenhouse insect-proof cage, tomato plants intercropped with wild oregano from southern Martinique had 1.5 fewer adult whiteflies than tomato plants grown alone after 96 h of exposure. The behavior of *B. tabaci* appears to be influenced by the origin of the plant	Pouët et al., 2022
Coriander (*C. sativum*); Greek basil (*Ocimum minimum* Labiatae)	Intercropping	Open field; greenhouse	Planting tomatoes with coriander and Greek basil resulted in an 84% and 79% reduction in adult *B. tabaci* populations compared to monocropping	Carvalho et al., 2017
English marigold (*Calendula officinalis* L.)	Intercropping	Greenhouse	Intercropping significantly inhibits the population development of *Trialeurodes vaporariorum* Westwood	Conboy et al., 2019
Marigold (*Tagetes erecta* L.)	Intercropping	-	Intercropping, combined with one release of *Trichogramma chilonis* Ishii, the application of Nimbecidine, and a spray of *Bacillus thuringiensis* Berliner kurstaki, significantly reduces the number of eggs and larval population of *H. armigera*, with minimal negative impact on non-target organisms	Khokhar and Rolania, 2022

(Continued)

TABLE 2 (Continued)

Companion species	Crop system	Infrastructure	Benefit	References
Sainfoin (*Onobrychis viciifolia* Scop.)	Intercropping	-	Intercropping reduces the number of *T. absoluta* eggs, larvae, and galleries. It also increases the diversity index for the species composition of *T. absoluta* predators, such as *Orius niger* Wolff and *N. tenuis*, and raises the larval parasitism rate	Zarei et al., 2019
Coriander (*C. sativum*)	Intercropping	-	The presence of coriander plants created visual and olfactory barriers that made tomato plants less attractive to *B. tabaci*. As a result, intercropping with overhead sprinkler irrigation reduced the colonization levels of *B. tabaci* and decreased the incidence of Begomovirus-infected plants	Togni et al., 2018
Coriander (*C. sativum*); marigold (*Tagetes minuta* L.); sorghum (*Sorghum bicolor* L.)	Crop mixture (surrounding crop)	-	Intercropping reduced the incidence of thrips, resulting in a decrease in the percentage of plants and fruits with symptoms of viral disease. Additionally, it led to a reduced incidence of drilling by *Neoleucinodes elegantalis* Guenee	Gomes et al., 2012
Coriander (C. sativum) and dill (Anethum graveolens L.)	Intercropping	-	The reduction in whitefly population between the intercropping treatments ranged from 56.00% to 72.00% with coriander and 33.00% to 58.00% with dill, when compared to tomato as a sole crop	Padala et al., 2023
-	Field margin	-	Field margins increased the densities of natural enemies, reduced pest damage to the crop, decreased weed cover, and consequently, resulted in higher yields in tomato crops. Pest control was more effective during the late crop stage compared to early-season sampling	Segre et al., 2020
Soil-borne pathogens				
Maize (*Z. mays*)	Cover crop	-	Crop rotation enhances the effectiveness of the antagonist *Pasteuria penetrans* in suppressing root-knot nematode (RKN) populations in subsequent crop cycles	Shahid et al., 2020
	Crop sequence	Glasshouse; open field	The application of crop rotation consistently led to a reduction in the numbers of second-stage juvenile RKN on roots, combined with the benefits of the *Pochonia chlamydosporia* biological control agent	Luambano et al., 2015
Sunn hemp (*Crotalaria juncea L.*)	Cover crop	-	Sunn hemp is effective in the suppression of *Meloidogyne incognita* Kofoid and White	Marquez and Hajihassani, 2023
Nemat (*Eruca sativa* Mill.); canola (*Brassica napus* L.)	Cover crop; crop sequence	Greenhouse	Using nemat as a cover or rotation crop suppressed *Meloidogyne javanica*. In the case of *Criconemoides xenoplax*, the population declined over time when canola was implemented as a cover crop	Kruger et al., 2015
Wheat-resistant cultivar Lassik (*Triticum aestivum* L.)	Crop sequence	Greenhouse	Tomato exhibited reduced root galling by RKN when grown in soil from micro plots that had previously included RKN-resistant wheat	Williamson et al., 2013
Castor (*Ricinus communis* L.)	Intercropping	Greenhouse	The root exudates from intercropped plants reduced the nematode soil population and inhibited *M. incognita* infection by regulating nematode chemotaxis	Dong et al., 2018
Crown daisy (*Chrysanthemum coronarium* L.)	Intercropping	Greenhouse	The potent bioactivity of lauric acid, which is a specific crown daisy root exudate, serves as both a lethal trap and a repellent for *M. incognita*. The reaction depends on the concentration of the exudate	Dong et al., 2014
Black-jack (*Bidens pilosa* L.)	Intercropping	-	Intercropping reduced the number of galls and egg masses on *M. incognita* susceptible host plants by 3–9 times compared to the control group	Kihika-Opanda et al., 2022
Chinese leek (*Allium tuberosum* Rottler ex Spreng)	Intercropping	Greenhouse	The gall indexes of tomato plants intercropped with Chinese leek decreased by 41.1%. Chinese leek exhibits high resistance to RKNs, demonstrates strong nematocidal activity against *M. incognita*, and significantly reduces the incidence of diseases caused by nematodes	Huang et al., 2016
Moringa (*Moringa oleifera* Lam.)	Intercropping	Greenhouse	The lowest values of *M. incognita* and *Rotylenchulus reniformis* Linford and Oliveira, as well as their rate of increase and root gall index, were observed when the highest number of moringa seedlings per pot (four) were grown	Ismail, 2013

(Continued)

TABLE 2 (Continued)

Companion species	Crop system	Infrastructure	Benefit	References
Marigold (*T. erecta*); garlic (*Allium sativum* L.)	Intercropping; crop sequence	Greenhouse	Intercropping tomato with antagonistic marigold, followed by tomato intercropped with garlic, resulting in a reduction in root galls, egg masses, and J2 nematodes of RKNs per plant compared to tomato monoculture	Miheret et al., 2019
Arugula (*E. sativa.*)		-	The use of fresh arugula as a soil amendment reduced tomato nematode infection. Therefore, it can be considered a promising companion plant for tomato growers to control *M. incognita*	Aissani et al., 2015
Marigold (*Tagetes patula* L.); basil (*O. basilicum*); lettuce (*L. sativa*); white mustard (*Sinapis alba* L.)	Intercropping	Greenhouse	All the tested companion plants suppressed the development of *Meloidogyne* spp., with white mustard and marigold showing the highest effectiveness at 53.45% and 46.38%, respectively	Tringovska et al., 2015
Garlic (*Allium sativum* L.); Madagascar periwinkle (*Catharanthus roseus* L.); Yarrow (*Achillea millefolium* L.)	Intercropping	Laboratory; greenhouse	The root exudates of garlic and yarrow did not attract the J2s of *M. javanica*. The root exudates of marigolds were highly and Madagascar periwinkle slightly attractive; but despite their attractiveness, J2s did not complete their cycle inside the roots in marigolds and Madagascar periwinkle	Cavalcanti et al., 2023
Rye (*S. cereale*); Indian mustard (*B. juncea*); white mustard (*S. alba*); arugula (*E. sativa*)	Cover crop (Anaerobic soil disinfestation)	-	The mean populations of *Rhizoctonia solani* Kuhn throughout the year were lower than those in the untreated control and similar to those in the biofumigant control when using cover crops such as mustard/arugula and rye for anaerobic soil disinfestation treatment	McCarty et al., 2014
Celery (*Apium graveolens* L.)	Crop sequence	Greenhouse	Rotating with celery may increase the abundance and diversity of fungi in continuous tomato cropping substrates while reducing the relative abundance of harmful fungi such as *Pseudogymnoascus, Gibberella*, and *Pyrenochaeta*	Lyu et al., 2020
Rice (*Oryza sativa* L.)	Crop sequence	-	Crop sequencing reduced the presence of the pathogenic fungal genus *Fusarium* and increased the presence of potentially beneficial bacterial phyla, such as Acidobacteria and Chloroflexi. The total phosphorus content was a determining factor for both bacterial and fungal communities	Ma et al., 2021
Wheat (*T. aestivum*)	Crop sequence	-	After 4 years of consecutive rotation, there was an increase in the soil's suppressive response against *F. oxysporum*, a decrease in their pathogenicity and abundance in the tomato rhizosphere, and an increase in the growth of tomato shoots	De Corato et al., 2020
Basil (*O. basilicum*)	Intercropping	Greenhouse	Intercropping increased plant biomass and significantly reduced the severity of *F. oxysporum* in tomatoes. Furthermore, the addition of arbuscular mycorrhizal fungi to the intercrop enhanced the host plant's tolerance by influencing tomato root morphology and exudation dynamics	Raza et al., 2022
Potato-onion (*A. cepa*)	Intercropping	-	Intercropping increased the relative abundances of certain taxa and various operational taxonomic units that have the potential to enhance plant growth. Simultaneously, it decreased the relative abundances of some potential plant pathogens, such as *Cladosporium*	Li et al., 2020
		-	Intercropping can enhance tomato resistance against *F. oxysporum* by improving soil enzymes and increasing antifungal enzyme activity in the soil	Sweellum and Naguib, 2023
		Greenhouse	Intercropping altered the composition of the tomato rhizosphere microbiome by increasing the colonization of specific *Bacillus sp.*, which has been shown to reduce the growth of *V. dahliae* and induce systemic resistance in tomato plants	Zhou et al., 2023
		Greenhouse	Root exudates from tomatoes accompanied by potato-onion reduced the mycelial growth and spore germination of *V. dahliae*. However, these effects were not observed with root exudates from potato-onion alone	Fu et al., 2015
	Crop sequence	-	The root exudates from Chinese onion accessions increased tomato growth and reduced the incidence of *F. oxysporum*	Liu et al., 2013
	-	Laboratory	Root exudate inhibited the growth of *V. dahlia*	Li et al., 2018

(Continued)

TABLE 2 (Continued)

Companion species	Crop system	Infrastructure	Benefit	References
Marigold (*T. erecta*)	Intercropping	-	Intercropping with plastic mulching reduces disease intensity compared to tomato monocropping. Marigold serves as a barrier to the movement of conidia, and plastic mulching creates a microclimate that reduces the germination of *Alternaria solani* spores	Jambhulkar et al., 2015
		-	Intercropping with the use of plastic mulch reduces the intensity of *A. solani*. Marigold serves as a barrier to the movement of conidia, and plastic mulch prevents evapotranspiration, reducing canopy relative humidity	Jambhulkar et al., 2016
Tall fescue (*F. arundinacea*)	Intercropping	Greenhouse	Intercropping tomatoes with tall fescue resulted in a reduced incidence and severity of *R. solani*, and the antifungal activities of root exudates from both species increased in the intercropping system	Zhou et al., 2019
Sunn hemp (*C. juncea*); Japanese millet (*Echinochloa crusgalli* L.)	Cover crop	-	In monoculture, the disease incidence was 33%, whereas in the rotation with sunn hemp and Japanese millet, it decreased to 9%. These benefits continued into a second season, with a 17% reduction in *Ralstonia solanacearum* Smith in the rotation plots. Furthermore, tomato plants in the rotation exhibited lower levels of root galls caused by *M. incognita* infection	Chellemi et al., 2013
Weed and parasitic plants				
Hairy vetch (*V. villosa*)	Cover crop	-	Hairy vetch, when used as a cover crop, helps reduce weed growth	Campiglia et al., 2015
Soybean; maize; sweet corn; bean	Crop sequence	-	Crop rotation reduces volunteer plants in tomato crops and can also decrease the sources of inoculum for diseases transmitted by seeds, such as bacterial spots caused by *Xanthomonas perforans* Jones	Moura et al., 2020
V. villosa; *Vicia sativa* L.; *Secale cereale* L.; x *Triticosecale* Wittmack	Cover crop	-	Cover crops reduced weed dry weight in all tillage systems and increased the nitrogen level in tomato leaves. Soil nitrogen and organic carbon contents remained unaffected throughout the experiments	Samedani and Meighani, 2022
Vigna sinensis L.; *Hibiscus sabdariffa* L.; *H. vulgare*; *Sorghum vulgare* Pers.	Crop sequence	Glasshouse	Tomato cultivation following service species resulted in increased tomato growth and improved control of *Orobanche*	Qasem, 2019

The secretion of phenolic compounds, essential oils, and volatile organic compounds helps the companion plants to act as repellents or olfactory barriers. This mechanism can also attract beneficial organisms, to which the companion plants provide additional resources such as food and shelter (Abad et al., 2020; Castillo et al., 2022). Therefore, aromatic plants are commonly selected as companion plants for pest management (Carvalho et al., 2017; Conboy et al., 2019).

The depletion of natural landscape habitats, linked to monocultures and agricultural intensification, has increased pest pressure (Balzan et al., 2015). One approach to enhance habitat complexity is the implementation of field margins, which provide flowering resources and alternate prey necessary to enhance natural enemies' abundance and richness (Segre et al., 2020). Plants with strong scents and abundant nectar are generally used for the margins to complement the existing natural diversity (Balzan and Moonen, 2014; Foti et al., 2019). Certain plant families, such as Asteraceae, Fabaceae, and Apiaceae, have demonstrated the ability to foster a reservoir of parasitoids and predators (Kati et al., 2021). It's worth noting that the studies we reviewed primarily focus on observations made in open fields and within ~200 meters from the margins.

Other cropping systems, such as intraspecific mixtures and crop sequences, have also shown promise in mitigating damage caused by aerial pests (Ingerslew and Kaplan, 2018; Miano et al., 2022). However, a more comprehensive understanding of their benefits is needed.

3.2 Soil-borne pathogens

Monoculture reduces microbial diversity and soil organic matter, consequently giving rise to soil-borne pathogens such as fungi, bacteria, actinomycetes, and nematodes (Hooper et al., 2000; Lyu et al., 2020). According to this review, in the context of tomato crops, nematodes and fungi have been the primary focus of research.

Among the most common pathogenic nematodes affecting tomato crops are the root-knot nematodes (RKN), belonging to the genus *Meloidogyne* (Seid et al., 2015). Several cultivation systems have been employed to manage them, including cover cropping, crop sequencing, and intercropping. For crop sequencing, companion plants from the Poaceae family, such as wheat and maize, have been utilized; in the maize inclusion case, the presence and effectiveness of antagonists or biological control agents like *Pasteuria penetrans* and *Pochonia chlamydosporia* are enhanced and resulted in a 72% decrease in numbers of egg masses, 38% in root galling and 46% regarding female nematode populations over the control after the final harvest (Luambano et al., 2015; Shahid et al., 2020). In the case of cover crops, plants from the Brassicaceae family offer a biocidal effect due to the release of specific biologically active compounds during maceration and incorporation processes (Kruger et al., 2015). Also, Fabaceae plants, such as *C. juncea*, are employed as cover crops (Marquez and Hajihassani, 2023), which favor the abundance and richness of soil communities, which results effectively in suppressing *M. incognita* (Scaglione et al., 2023). In the intercropping system, species like *Allium tuberosum* Rottl, *Ricinus communis* L., *Chrysanthemum coronarium* L., and *Bidens pilosa* L. release exudates that inhibit egg hatching or act as nematicides (Dong et al., 2014, 2018; Huang et al., 2016; Kihika-Opanda et al., 2022).

While companion species in intercropping systems offer benefits for controlling soil pests, they sometimes can lead to reduced yields of the main crop due to competition among plants (Tringovska et al., 2015). In such cases, it is essential to conduct studies to identify the minimum population of companion plants that can continue to provide benefits without significantly affecting tomato yield (Castillo et al., 2022).

To control pathogenic fungi, crop rotation and intercropping stand out as widely studied cropping systems; particularly, crop rotation enhances the suppression of pathogens and improves tomato plant growth by inducing changes in microbial composition and soil chemical parameters (De Corato et al., 2020). For instance, *Apium graveolens* L., due to its potent allelochemicals that alter soil pH, enhances the abundance and diversity of fungi, reducing the abundance of harmful organisms (Lyu et al., 2020).

Both intercropping and crop rotation induce changes in microbial communities and improve the soil environment (Li et al., 2020; Zhou et al., 2023). Additionally, they boost tomato resistance against pathogens. For example, when the tomato grew with *A. cepa*, it exhibited heightened activity in antifungal enzymes and increased content of phenols bound to the cell wall, effectively curbing the growth and spread of *Fusarium oxysporum* Schl. (Sweellum and Naguib, 2023). Moreover, root exudates from tomatoes accompanied by *A. cepa* significantly inhibit the mycelia growth and spore germination of *Verticillium dahlia* Kleb (Fu et al., 2015). Another way in which mixed cultures reduce pathogen damage is by acting as barriers to the movement of conidia, as demonstrated by the use of *Tagetes erecta* L. against *Alternaria solani* (Jambhulkar et al., 2015).

3.3 Weeds, volunteer plants, and parasitic plants

Weeds compete with crops for essential resources such as light, water, and nutrients; additionally, they can serve as alternative hosts for crop pests and pathogens (Moura et al., 2020; Christina et al., 2021). The few existing studies provide a glimpse of the benefits of cover crops in weed management, mainly in no-tillage tomato crops, but they are not sufficient to understand all the variables that may influence the success of this practice against this type of stress, so there are still challenges regarding the use of cover crops in weed control (Campiglia et al., 2015; Roberts and Mattoo, 2018; Samedani and Meighani, 2022).

In the case of parasitic plants, *Orobanche spp*. is a problematic parasitic species for agriculture that is difficult to control; trap species such as *Vigna sinensis* L., *Hibiscus sabdariffa* L., *H. vulgare*, *Sorghum vulgare* Pers. stimulate the germination of parasite seeds and then destroy them before the parasite flowers, reducing the parasite in the subsequent tomato crop by 73% (Qasem, 2019).

Volunteer plants, which can sprout from fruit that remains in the soil after mechanical harvesting of tomato, represent a source of inoculum for many crop diseases, such as *Xanthomonas perforans* Jones; in this regard, when tomatoes grow with soybean, corn, sweet corn, and bean, the number of volunteer plants and sources of *X. perforans* inoculum is reduced (Moura et al., 2020).

4 Conclusions and future directions

Biodiversity offers numerous advantages for tomato cultivation. These benefits directly mitigate the impacts of various types of biotic and abiotic stress and indirectly align with agroecological principles such as reduced inputs, improved soil health, synergy, and recycling. The most extensively studied stressors encompass: (1) Soil nutrient deficiency: Often addressed with companion species like *V. villosa*; (2) Aerial Pests: Effectively managed with aromatic plants such as *C. sativum*; and (3) Soil-Borne Pathogens: *A. cepa* is a common choice for combatting pathogenic fungi. Different cropping systems come into play, with cover crops being prominent for nutritional deficiencies and intercropping for aerial pests and soil-borne pathogens.

Future research should focus on assessing companion species that can mitigate less explored stress types such as cold temperatures, heavy metal contamination, salinity, water scarcity, and weed infestations. These evaluations should consider factors like species distribution, plant quantities, and the cultivation system that maximizes companion species benefits.

To select companion species for evaluation it's recommended to incorporate local knowledge through participatory methods while also developing general guidelines or principles for species selection. A couple of proposals arising from this review are: (1) Aromatic plants show significant potential in managing aerial pests and soil-borne disease pathogens, and (2) Cover crops contribute directly and indirectly to provide nutrients. Using legume-cereal mixtures to balance the carbon-nitrogen ratio prevents nutrient leaching.

Author contributions

VC-L: Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing, Conceptualization. CG-E: Formal analysis, Methodology, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing –

review & editing. RP-P: Conceptualization, Formal analysis, Resources, Supervision, Validation, Writing – review & editing. CR: Conceptualization, Formal analysis, Resources, Supervision, Validation, Visualization, Writing – review & editing. JÁ-L: Data curation, Formal analysis, Methodology, Software, Supervision, Validation, Visualization, Writing – review & editing. IM: Data curation, Formal analysis, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing. LB-O: Data curation, Methodology, Project administration, Software, Supervision, Validation, Visualization, Writing – review & editing. FG-P: Data curation, Formal analysis, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing. JD-J: Data curation, Formal analysis, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing. NL-V: Data curation, Formal analysis, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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