Legacies at work: plant-soil-microbiome interactions underpinning agricultural sustainability

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Opinion

Legacies at work: plant–soil–microbiome interactions underpinning agricultural sustainability

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Agricultural intensification has had long-lasting negative legacies largely because of excessive inputs of agrochemicals (e.g., fertilizers) and simplification of cropping systems (e.g., continuous monocropping). Conventional agricultural management focuses on suppressing these negative legacies. However, there is now increasing attention for creating positive above- and belowground legacies through selecting crop species/genotypes, optimizing temporal and spatial crop combinations, improving nutrient inputs, developing intelligent fertilizers, and applying soil or microbiome inoculations. This can lead to enhanced yields and reduced pest and disease pressure in cropping systems, and can also mitigate greenhouse gas emissions and enhance carbon sequestration in soils. Strengthening positive legacies requires a deeper understanding of plant–soil–microbiome interactions and innovative crop, input, and soil management which can help to achieve agricultural sustainability.

Highlights

Agricultural intensification leaves negative legacies that influence soil microbiomes, weakening their capacity to deliver multiple soil ecosystem functions.

Innovative agricultural management can create positive above- and belowground legacies that improve agricultural sustainability.

Deciphering the cascading effects of plant–soil–microbiome interactions will promote the innovation of soil, input, and crop management.

In-season interspecific interactions in mixtures can create positive legacies for subsequent crops.

Legacies in terrestrial systems

Terrestrial plant communities are structured by many interactions that occur between plants and above- and belowground multitrophic communities. However, the current plant community can also be influenced by the plants that were growing previously at the same location and the multitrophic interactions that occurred previously on those plants. An increasing number of studies are now showing that such legacies, defined as anything that is transmitted by or received from the past, can have a significant impact on the current and future performance of plants. These legacy effects have been extensively studied in social sciences in the context of human wellbeing [1], but legacies can also play pivotal roles in both natural and agricultural systems [2]. Agricultural intensification has tremendously increased crop yield and has successfully met the increasing demand for food in past decades, yet excessive inputs of agrochemicals (e.g., synthetic fertilizers) can create severely negative legacies that result in biodiversity loss, and ultimately in ecosystem deterioration and environmental pollution [3], even though the negative effects are ecosystem-specific [4].

Soil legacies

In the past decade the role and importance of belowground plant–soil legacies has become a central theme among ecologists. Plants can alter the abiotic and biotic components of the soil ecosystem and this can result in soil legacies that facilitate or inhibit the growth of succeeding plants. The nature of such a soil legacy effects can function through changes in inoculum densities of soil pathogens or symbiotic mutualists [5,6] via the accumulation of **allelochemicals** (see Glossary) [7] or via changes in the availability of resources such as soil-available nitrogen (N) or changes in soil organic matter (SOM) [8]. A phenomenal amount of work over the past years shows that such plant-induced soil legacies occur in many ecosystems [2]. These plant–soil legacies can persist in the soil during an entire season or even for several years or longer,

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and therefore can have long-term consequences for plant community diversity, composition, and productivity. For example, a recent study with sequential monocultures showed that plant-specific effects of a first monoculture on the fungal community in the soil were still detected 6 months after the second monoculture had been planted in that soil [9].

In an agricultural context, the role of soil legacies has long been recognized and it is well known that the way the soil is treated now can greatly influence the performance of subsequent crops. A famous example of a soil legacy is the phenomenon that repeatedly growing the same crop in the soil leads to a reduction in crop yield and increased prevalence of soil-borne diseases. This phenomenon is known as soil sickness, soil fatigue, or negative **plant–soil feedback** [10] (Box 1). These negative soil legacies arising from continuous monocropping are caused by

Box 1. Negative and positive legacies in agricultural systems

Several crops grown in open-field and protected cultivation have experienced severe obstacles to continuous cropping. These crops comprise taxa such as Leguminosae (e.g., soybean), Brassicaceae (e.g., cabbage), Compositae (e.g., chrysanthemum), Solanaceae (e.g., tobacco), and Chenopodiaceae (e.g., sugarbeet). A wide range of sustainable management practices such as diversified cropping systems and microbiome inoculations have been proposed to enhance the positive legacies through influencing plant–soil–microbiome interactions (Figure I).

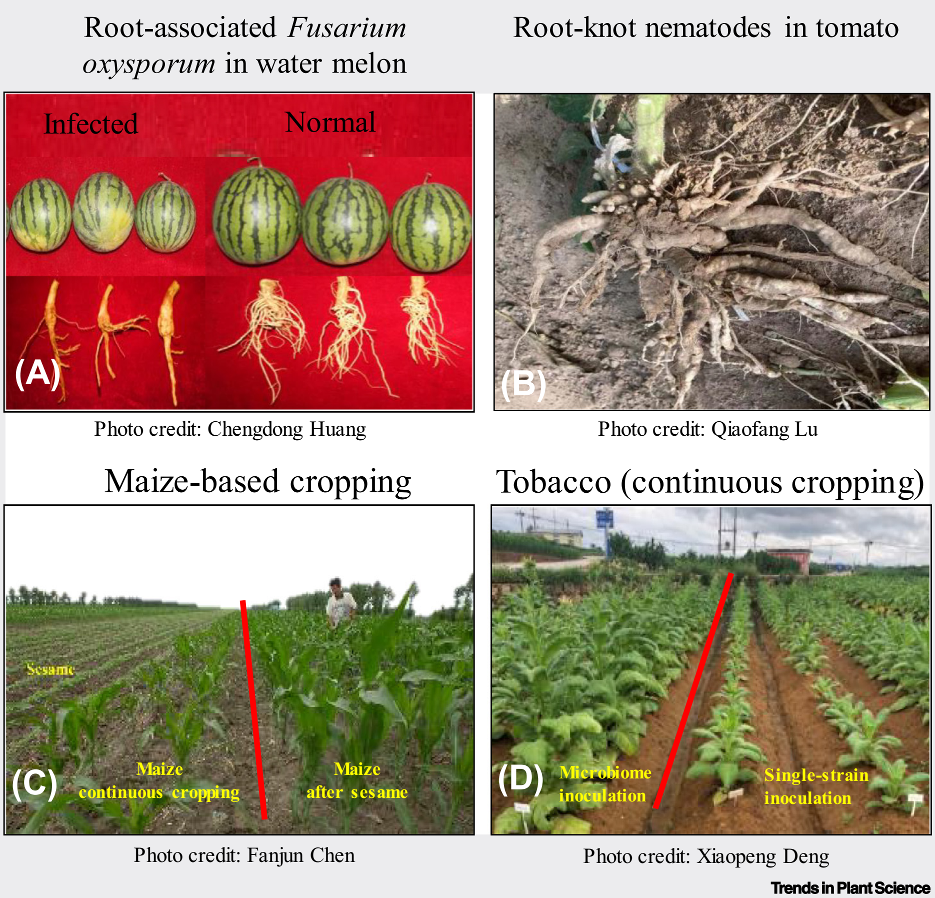

Figure I. Examples of negative and positive legacies on arable and cash crops. (A) Root-associated *Fusarium oxyporum* infesting watermelon roots. (B) Nematodes parasitizing tomato roots and deforming roots with knots. (C) Maize performed better after sesame than after maize. (D) Whole-microbiome inoculation promoted tobacco growth more effectively than single-strain inoculation.

Glossary

Allelochemicals: a toxic chemical compound produced by a plant to defend itself against antagonists such as herbivores, pathogens, competing plants.

Arbuscular mycorrhizal fungi (AMF): a group of fungi belonging to the Glomeromycotina phylum that establish endosymbiosis with land plants and form arbuscules within root cortical cells.

Intelligent fertilizers: a novel fertilizer product that can enhance the biological potential of plant roots and the microbiome to take up soil nutrients, while precisely matching the soil and climate conditions.

Parasitoid: an organism that lives in close connection with its host at the expense of the host, eventually resulting in host death.

Phytosiderophores: root exudates released by graminaceous species under iron- and zinc-deficiency stress that are important for the acquisition of iron.

Plant growth-promoting rhizobacteria (PGPR): bacteria that grow in association with a host plant and that can colonize plant roots and improve plant growth.

Plant–soil feedback: a phenomenon where plant species can influence soil abiotic and biotic properties which can then affect the performance of subsequent plants.

nutrient imbalance, the presence of **allelochemicals** in the soil, soil physical barriers (e.g., soil compaction), and especially soil biotic effects (e.g., the build-up of pests and pathogens). For xample, the negative legacies of a simplified assembly of soil microbial communities owing to continuous peanut monocropping can downregulate gene expression needed for plant hormone production, consequently impacting on peanut growth and physiology [11]. However, continuous cropping may not necessarily lead to long-lasting disease problems, and hence to negative legacy effects, since specific antagonistic microbial consortia may be activated and enriched in continuous monocropping to form pathogen-suppressive traits in soils during the disease outbreak period [12]. Furthermore, soil pathogens can not only induce a disease-suppressive soil microbiome as the first line of defense but also activate the protection occurring in the endophytic root microbiome [13]. A recent review paper proposed that interactions between plant roots, microorganisms, and macrofauna can construct complex soil structure, thus creating diverse redox potential (Eh)/pH niches to harbor a diversity of microorganisms as the key determinant of soil suppressiveness [14].

Soil legacies can also be mediated by organisms other than plants and soil organisms. For example, above- and belowground herbivory by insects on ragwort plants exerts soil legacy effects via changes in the composition of soil fungi. This in turn influences the concentration of alkaloids in plants growing in that soil later, ultimately affecting aboveground plant–herbivore–**parasitoid** interactions on those plants [15]. Moreover, changes in the environment such as extreme climate events can create soil legacies [16–19]. For example, plant–microbiome interactions break down under severe or long-term drought, and this can lead to plant and microbial death which consequently affects plant–microbe interactions in later growing plants [20]. In addition to soil legacies, aboveground legacies, for example, due to the return of straw that carries pests (e.g., eggs) or pathogens (e.g., spores), can also increase the disease infection rate during the following cropping cycle. As legacy effects can have a variety of origins, future research should attempt to decipher the relative importance of these origins in a specific system, and this would help to identify an effective solution to avoid the negative legacies.

Conventional agricultural management has focused on suppressing negative legacies or avoiding the buildup of negative legacies through applying pesticides to suppress pests or diseases and through incorporating crop-rotation schemes to avoid continuous monocropping. By growing different crops sequentially, negative legacies can be suppressed or can be prevented from building up [21]. For example, a five-crop rotation (corn–soybean–wheat plus two cover crops) can increase disease-suppressive functional group *prnD* gene abundance by 9% compared with monocultures. Recently, the concept of agroecological approaches such as crop diversification, no-till, and organic agriculture have been widely adopted to create positive legacies [22,23]. This development focuses on improving conditions in the soil such that this soil becomes better or healthier for the next crop. We illustrate how innovative management of crops, inputs, and soils can create positive legacies that can improve agricultural sustainability.

Creating positive legacies for agricultural sustainability

Engineering of soil legacies can enhance agricultural sustainability in various ways (Figure 1, Key figure). A wide range of management practices such as selection of crop species/genotypes, diversification of cropping systems, introduction of novel fertilizers, and soil/microbiome inoculation are available that can create or enhance positive legacies and/or reduce the negative legacies through influencing plant–soil–microbiome interactions [24–26] (Box 1). The resulting aboveground effects (e.g., reduced population densities of pests and inoculum densities of diseases in crop residues) and belowground effects (such as better soil structure and changed soil microbiome) then, in turn, can become legacies that benefit the performance of the succeeding

Key Figure

Manipulation of agricultural management by optimizing positive legacies for agricultural sustainability

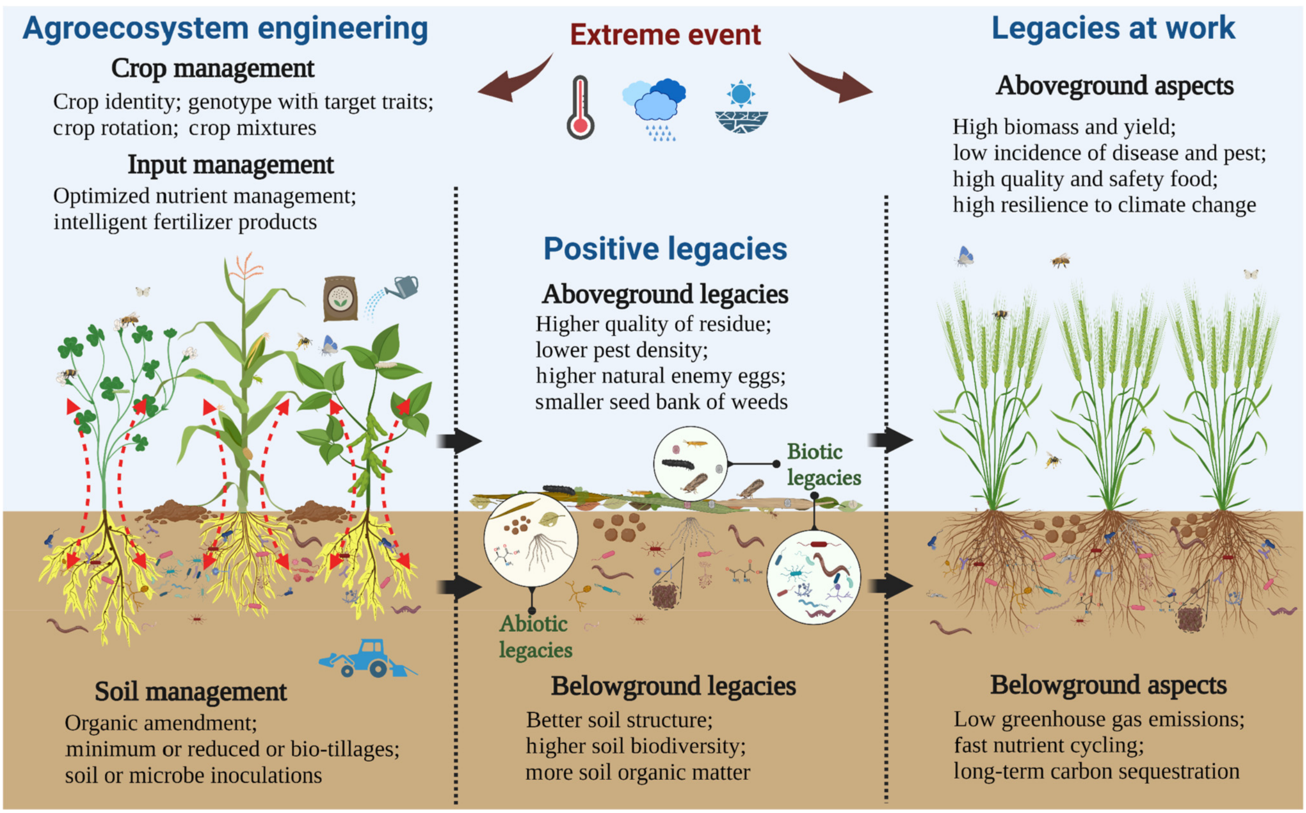

Figure 1. Optimized agricultural management consisting of species/genotype selection, crop diversification, inputs, and soil/microbiome management will create positive above- and belowground legacies that can influence the production of high-quality and nutritious food, create healthy soils, and can increase the resilience of agroecosystems to climate change and extreme climatic events such as drought. Figure created using BioRender (https://biorender.com/).

crop such as resistance to extreme climate events, pests, and diseases, and can result in reduced greenhouse gas emissions or long-term soil carbon (C) sequestration.

Selecting crop species or genotypes to create positive legacies

Plant species and genotypes of a single species show natural variation in traits related to root architecture, morphology, physiology, and biotic interactions that drive key ecosystem processes and functions such as resource acquisition and utilization, nutrient cycling, and disease suppression as well as the structural stability of soils [27,28]. This can help plants to occupy different ecological niches, allowing positive legacies to occur. For example, deep-rooting annual crops such as sunflower and sugarbeet, as well as perennial crops such as lucerne that can reach rooting depths, can acquire resources at depth such as water infiltrated from irrigation and nutrients from fertilization that leach to the deeper layers in the soil [29]. Hydraulic redistribution by deep-rooted species to the topsoil can promote early-stage plant growth of the next crop under drought conditions. Another example is that maize roots can grow prolifically with newly formed nutrient patches or tunnels created by faba bean roots, and that this contributes to higher maize biomass [30].

Crop species can also affect the performance of subsequent crops via changes in soil structure. For example, compacted soil can limit root growth either through imposing mechanical resistance to roots or by creating locally high concentrations of ethylene which can act as a signal restricting root growth of rice [31]. Thus, improved soil structure will allow roots to penetrate into soil pores, thus enabling intensified interactions with microorganisms. Bio-tillage through growing crops with high root-penetrating capacities can on the one hand improve soil structure, and on the other hand form the biopores when roots are dead and decomposed, thus providing a favorable environment (e.g., nutrients) for the following crop [32]. For example, growing deep-rooting chicory and lucerne can construct soil pore structures, whereas bio-tillage with black oats and forage radish can enhance soil organic carbon (SOC) stocks that subsequently improve the root growth and yield of wheat and soybean [33].

Crop species and genotype identity can be an important driver of changes in soil microbiomes [26,34]. Therefore, a large number of studies are now advocating that species or genotypes should be selected that create positive soil microbial legacies [35–37]. Most studies examining how the species identity of a crop influences soil legacies have so far focused on changes in the soil microbiome. However, several recent studies show that such legacies can also be created via chemical compounds [38]. Secondary compounds released by plants into the soil can be acquired from the soil by other plants and incorporated into plant tissues. For example, in a tobacco–rice rotation system, nicotine, that is exuded by tobacco in the soil, can be found in later rice plants where it then increases resistance against aboveground insect pests [39]. Similarly, several recent studies have demonstrated that a group of secondary plant compounds, the benzoxazinoids that are released by roots of cereals, can influence plant performance and plant–herbivore interactions of the next generation through changes in the composition of rhizosphere microbiota [40–42]. More work will be necessary to better understand how common these plant–soil–plant transfers of chemical compounds are, and how important such chemically mediated soil legacies are for the resistance of succeeding plants against pests and diseases.

Microbial legacies via root exudates can be influenced by multitrophic interactions that occur above- and belowground. For example, by adjusting the composition of root exudates, plants can adjust their root microbiome upon pathogen infestation and specifically recruit a group of synergistic bacteria that induce resistance in the plant or promote plant growth. Such changes in the soil microbiome can then potentially increase the chance of survival of their offspring that will grow in the same soil [43]. How general this pattern is among plant species and pathogen or herbivore species is not yet known [44].

Designing diversified cropping systems for positive legacies

Temporal crop diversification such as crop rotation schemes can enhance the yield and the stability of yield over seasons, and can improve soil ecosystem services [23,45,46]. However, only a few studies so far have attempted to analyze both the immediate effects of crop rotations on soil ecosystem functioning and the legacy effects for subsequent crops. Inclusion of a bioenergy crop of willow short rotation coppice in rotation led to higher SOC concentration and soil biodiversity in topsoils owing to a greater amount of high-quality leaf fall than inclusion of maize in rotation in a 6 year field experiment. Consequently, wheat grown in willow-conditioned soils had higher biomass and better pathogen suppression than maize examined in a greenhouse experiment [47]. However, apart from the positive legacy effects on the productivity of following crops, diversification of rotations can also create negative legacies for other ecosystem services.

For example, changes in SOM and microbial properties influenced by ley grasslands introduced into crop rotations can lead to increased greenhouse gas emissions (e.g., N_2O) in the soil during the following arable crop [48–50]. Remarkably, which crops should succeed each other to promote desired ecosystem services is still poorly defined [36,51]. Obviously, there is an urgent need for more research on crop-specific effects on soil microbiomes and on the responses of other crops to those changes. Such information is essential to design optimal sequential crop combinations.

Cover crops are also a sustainable option to modify soil microbial communities [52,53]. Several studies have shown that the effects of cover crops on the soil microbiome, either directly or via decomposition of plant remains, can be used to enhance the tolerance of the succeeding cash-crop seedlings against pathogens [6]. Soil legacies can be created by living plants but also by plant residues, for example, root litter that remains in the field after harvest [54]. Cover crops can also create positive legacies by stimulating the decomposition of both high-quality and low-quality crop residues and influence soil C and N dynamics, subsequently promoting the growth of the following crop [55,56]. However, some non-mycorrhizal cover crops, such as canola and forage radish, can reduce **arbuscular mycorrhizal fungi (AMF)** root colonization and consequently decrease phosphorus uptake of the following maize [57]. Therefore, more insight into the functional traits of cover crops is key to creating positive soil legacy effects.

In addition to temporal crop combinations via crop rotation or cover crops, interspecific interactions between neighboring plant species (i.e., spatial crop combinations) can cause legacies that affect the following crop both via above- and belowground pathways. Intercropping maize with faba bean, for example, leads to an increase in the relative abundance of rhizobia and in a reduction in the relative abundance of pathogenic *Fusarium* in the soil in comparison to soils of monocultures of faba bean. This microbial legacy can contribute to the yield advantage in intercropping systems [58]. In four different decade-long field experiments, intercropping was found to enhance soil fertility, and this in turn resulted in higher and more stable crop yields [59]. However, neighboring plants can also facilitate disease transmission. For example, the fungal root pathogen *Rhizoctonia solani* can be transmitted between plant species as the host plant can act as a bridge to the next susceptible plant [60]. Positive legacies can be created via several pathways in which both above- and belowground interspecific interactions between neighboring species are involved (Box 2). A better understanding of the underlying mechanisms will be crucial for designing and optimizing temporal and spatial crop combinations – not merely for the current yield but also for consistent and long-term performance of crops in sustainable cropping systems.

Improving nutrient input management for positive legacies

Optimized nutrient management can sustainably increase crop yields, reduce N inputs, and enhance SOM accumulation [61]. For example, modern molecular approaches have revealed that optimal N fertilization fosters the amount of organic acids released by maize roots, which is associated with an increase in the abundance of **plant growth-promoting rhizobacteria (PGPR)** [62]. PGPR can further affect root system architecture by modulation of cell division and differentiation [63]. PGPR can directly facilitate nutrient acquisition or modulate phytohormone levels in plants or indirectly affect plant growth by suppressing various pathogens, enhancing the immune system, or improving resistance to environmental stresses [7]. For example, in the maize rhizosphere, Oxalobacteraceae are enriched via root-derived flavones, and this facilitates the development of lateral roots under optimized N management [64].

Fertilization can also indirectly affect the structure and function of soil microbiome through changes in their predators or parasites, thus exerting top-down control in regulating the structure

Box 2. Linking crop–crop interactions to legacies

Interspecific interactions between neighboring crop species can capture more resources (e.g., light, water, and nutrients), leading to increased biomass residues in soils and promoting long-term soil fertility (Figure I). Interspecific interactions in crop mixtures can promote beneficial soil biota while reducing the incidence of weeds, pests, and diseases both above- and belowground. Lower pest and disease damage in pre-crop residues and soils, as well as associated reduced pesticide use, will create a safe and healthy living environment for subsequent crops.

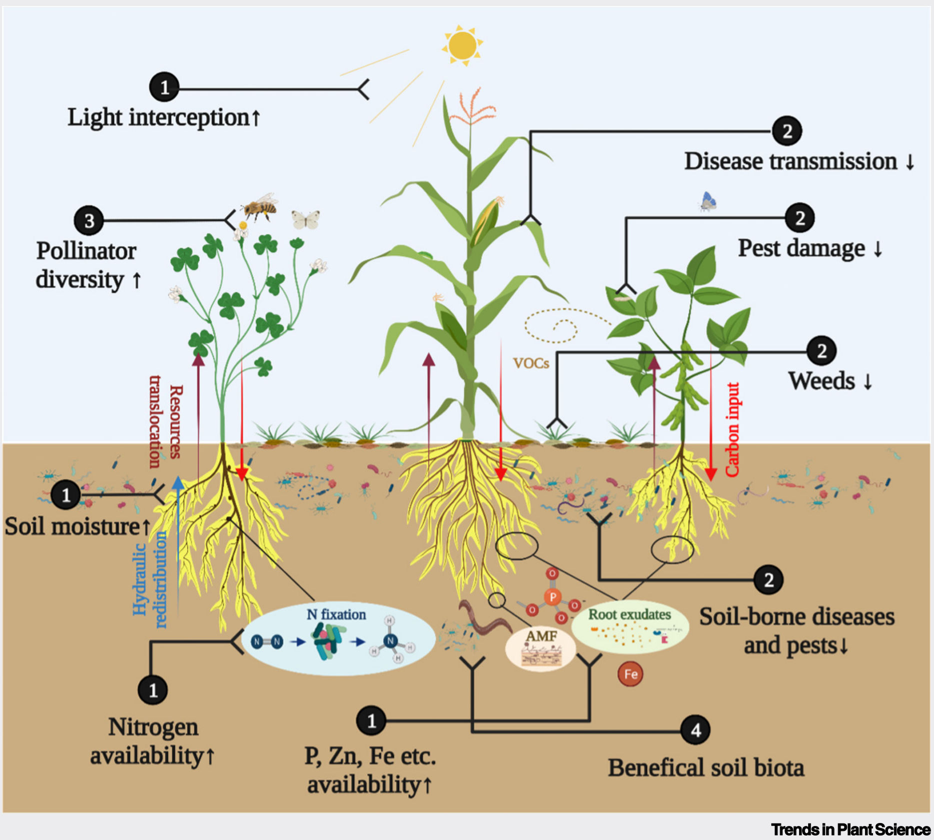

Figure I. Possible legacies created by multifaceted crop–crop interactions between neighboring crops. Interspecific interactions in crop mixtures can enhance productivity, stability, and soil ecosystem functions by facilitating resource use (❶), alleviating biotic stress (❷), and promoting insect pollinators (❸) and beneficial soil biota (❹), jointly creating positive legacies for following crops. Abbreviations: AMF, arbuscular mycorrhizal fungi; VOCs, volatile organic compounds. Figure created using BioRender (https://biorender.com/).

and function of soil microbiome [65]. For example, fertilization can significantly alter specific functional groups of protistan consumers and parasites, which in turn alter bacterial and fungal communities [66]. Moreover, fertilization can dramatically reduce the relative abundance of phagotrophic protists, and this can further influence microbiome-mediated soil ecosystem functions (e.g., nutrient cycling), consequently affecting the performance of follow-up crops [67]. Thus, stimulating the functions of soil biota via improved nutrient management can be a useful way to create positive legacies for subsequent crops.

Developing novel fertilizer products such as **intelligent fertilizers** can create positive legacies via building a healthy soil biotic environment for crops. Intelligent fertilizers can release nutrients in the interface where their coating interacts with plant roots and the soil, thus triggering the biological potential of plant roots and the soil microbiome to mobilize nutrients in soils. For example, plants can acidify soils and dissolve the coating material, thereby allowing the encapsulated nutrients to be released; this then nurtures adjacent plant roots and the local soil microbiome [68]. Soil application of a mugineic acid **phytosiderophore** analog, for example, can significantly enhance the availability of insoluble Fe in soil to overcome Fe deficiency [69]. The residual Fe-chelate may enhance the uptake of iron by the succeeding crop.

Steering soils and microbiomes for positive legacies

Incorporating organic or mineral amendments into the soil is an effective measure to create positive legacies. For example, applying organic materials (e.g., cattle manure) or mineral amendments (e.g., peat and vermiculite) can sustain the long-term productivity of wheat and maize through positive legacies on soil-quality parameters [70,71]. In addition to long-term fertility effects, organic amendments can suppress the occurrence or severity of diseases in following crops, for instance through changes in the soil microbiome [72]. For example, incorporating pineapple residues in soils highly infested with banana wilt disease can alleviate this disease via increases in the abundance of antagonistic fungal taxa [73]. Furthermore, conservation (minimum or reduced) tillage can modify soil structural and chemical parameters, further increasing copiotrophic microbial populations in the rhizosphere and their metabolic capacities [74]. It is currently unclear how long conservation tillage-induced microbial legacies last and to what extent they will influence subsequent plant growth.

An important practice to create positive legacies that is currently receiving a lot of attention is microbiome inoculation or whole soil inoculation [75,76]. For example, inoculation of AMF into the soil of watermelon can alleviate wilt disease by modulating the root exudation patterns of watermelon such that the exudates suppress colonization by the pathogen *Fusarium oxysporum* [77]. Apart from direct pathogen inhibition, bio-organic fertilizers inoculated with antagonistic microorganisms (e.g., *Bacillus* spp.) can induce suppressiveness of the soil by modifying the soil microbiome, for example, by stimulating indigenous soil *Pseudomonas* populations [78,79]. Inoculation of *Bacillus velezensis* in cucumber cultivations can induce the proliferation of native *Pseudomonas stutzeri* in the rhizosphere by releasing specific metabolites [80]. Synergistic interactions between inoculants and resident bacteria can promote plant health. Inoculation with microbes, for example, can also result in more beneficial rhizosphere communities that increase resistance to aboveground pathogens, thus leaving a positive soil-borne legacy that increases the fitness of subsequent plant generations [81].

We should note that studies on the inoculation of individual microbial strains often generate inconsistent results. Strains introduced to manipulate the soil microbiome often failed to flourish after inoculation into exogenous soils [82], whereas others have reported that the application of PGPB significantly improves plant growth [83]. However, the effectiveness of these type of inoculations in the field is typically very limited [84]. Currently, there is rapidly growing interest in understanding how to steer entire microbiomes in soils via inoculation so as to influence plant growth and health [37]. In that context, whole-soil inoculations have great potential as a tool to steer the soil microbiome and to create positive legacies [85]. In this approach, a thin layer of soil that contains a beneficial microbiome is collected from a donor site and is spread over the recipient agricultural soil or worked into the soil. For example, inoculation with soil containing different microbiomes resulted in different microbiomes in the recipient soil and induced chrysanthemum resistance against the thrips *Frankliniella occidentalis*, an important aboveground pest [37]. Clearly, with whole-soil inoculation, the entire microbiome is introduced. This type of inoculation can also introduce unwanted organisms such as pathogens, and growers may be wary to use such inocula. Further work will be necessary to develop ways to introduce safe whole-microbiome inocula and to study their persistence in the recipient soil.

Legacies at work in sustainable agriculture

Positive legacies in sustainable cropping systems function via enhanced resource availability, improved soil physical structure, specific chemical compounds, or microbial and faunal communities. We summarize three pathways in which management-induced positive legacies could be at work during the growth of subsequent crops (Figure 2). First, chemical compounds, microbiomes, or even entire soil food-webs from the preceding crop that are still in the soil can stimulate root growth and proliferation (e.g., lateral roots) of the succeeding crop [64,86]. These microbial legacies may further upregulate or downregulate the expression of plant genes governing the production of plant hormones (e.g., auxin, cytokinin) [11], consequently influencing the growth of the crop. Second, specific chemical compounds and pathogens may activate the plant immune system to produce defensive secondary metabolites that can protect against above- or belowground pests or diseases [42,87]. Finally, soil microbiomes (e.g., created by previous plants) can be transferred and incorporated into the plant and even into higher trophic levels such as insect herbivores [9,88].

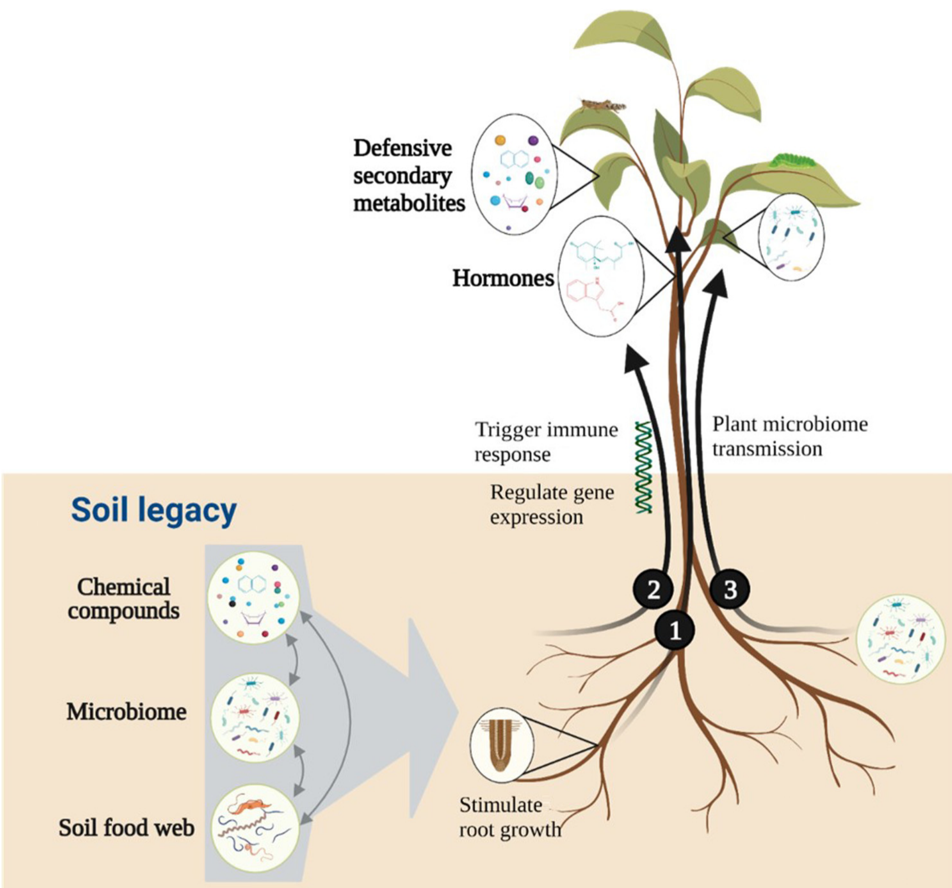

Figure 2. Three possible pathways through which legacies can influence subsequent crops. Chemical compounds, soil microbiomes, or the entire soil food web can affect the growth and defense of the subsequent crops by (1) stimulating root growth and subsequent plant growth, (2) producing defensive secondary metabolites to suppress aboveground pests, and (3) directly transmitting microbiomes from soil to plants. Figure created using BioRender (https://biorender.com/).

The role of 'soil legacy' microbes as endophytes inside plants or in the gut microbiome of insects is poorly understood, and there is an urgent need for a better understanding of these complex aboveground–belowground interactions. A better insight into the underlying mechanisms behind these legacy effects will be essential to achieve synergy between high agricultural productivity and ecosystem sustainability.

Concluding remarks and future perspectives

Steering above- and belowground legacies through ecosystem engineering such as crop/genotype selection, crop diversification optimization, improvement of nutrient input, application of innovative fertilizers, organic amendments, and microbiome inoculation can promote crop yield and environmental sustainability. As we argued before, plant–soil–microbiome interactions play a major role in these legacy effects.

We propose six themes for future research on legacies in agricultural systems. First, there is an urgent need to better understand how crops via legacies can benefit other succeeding crops. This would give rise to scientific basis for crop-rotation schemes [51]. The theory of plant–soil feedback is now widely applied in natural ecosystems and has great potential as an effective tool to design and optimize appropriate rotational sequences of crop species in agricultural systems [2]. Second, more emphasis should be placed on understanding the effects of innovative management practices (e.g., intelligent fertilizers, microbiome inoculation), as well as combinations of these agricultural management practices, on legacy effects on subsequent crop growth. Third, many studies focus on how legacies affect crop productivity and agricultural sustainability in relation to crop nutritional quality (e.g., micronutrient supply). How this is influenced by climatic conditions is less well understood, and the role of legacies in crop resilience to climatic events such as extreme droughts and warming necessitates further research [89]. Fourth, by being exposed to entire soil microbiomes, plants are continuously exposed to both positive (e.g., growth stimulation) and negative (e.g., pathogenic) effects from the microbiome. Changes in these microbiomes due to legacies also cause positive and negative effects on the plants. Most work on plant–microbe interactions has employed individual microbes, and how plants respond to this pleiotropy of effects is poorly understood. A better understanding of these multiple co-occurring influences on plant responses is urgently needed. Fifth, legacy effects are often affected by various origins or influencing factors (such as plant species, multitrophic herbivory, climate change, and management practices), and future research should study complex (rather than simplified) systems that resemble the real world, and should focus on deciphering their relative contributions. Last but not least, most studies focus on short-term legacies, and more insight in longer-term effects is urgently required. Long-term field experiments will be necessary to examine how long legacies will last as well to understand the dynamic patterns of these legacies. Although there are still many unknowns, positive legacies are essential to create a more sustainable agricultural system, and steering these legacies will be vital for future agricultural management (see Outstanding questions).

Outstanding questions

What soil legacies (biotic, abiotic) are created by different crops, under different cropping regimes, and by management practices?

Which combinations of management practices (crop, input, and soil) can maximize the positive legacies for subsequent crops and soil ecosystem functions?

How long will above- and belowground legacies last? What mechanisms determine the duration of the legacies?

Which soil microbial/microbiome indices can be used to predict positive legacies?

How do positive legacies confer resilience to extreme climatic events such as droughts and warming, and how can they help in developing climate-resilient agriculture?

What are the underlying mechanisms related to molecular interplay that regulate the complex plant–microbiome interactions?

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Declaration of interests

The authors declare no conflicts of interest.

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