

Accounting for soil biotic effects on soil health and crop productivity in the design of crop rotations

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Abstract

There is an urgent need for novel agronomic improvements capable of boosting crop yields while alleviating environmental impacts. One such approach is the use of optimized crop rotations. However, a set of measurements that can serve as guiding principles for the design of crop rotations is lacking. Crop rotations take advantage of niche complementarity, enabling the optimization of nutrient use and the reduction of pests and specialist pathogen loads. However, despite the recognized importance of plant–soil microbial interactions and feedbacks for crop yield and soil health, this is ignored in the selection and management of crops for rotation systems. We review the literature and propose criteria for the design of crop rotations focusing on the roles of soil biota and feedback on crop productivity and soil health. We consider that identifying specific key organisms or consortia capable of influencing plant productivity is more important as a predictor of soil health and crop productivity than assessing the overall soil microbial diversity *per se*. As such, we propose that setting up soil feedback studies and applying genetic sequencing tools towards the development of soil biotic community databases has a strong potential to enable the establishment of improved soil health indicators for optimized crop rotations.

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INTRODUCTION

Human population growth and changing consumption patterns affect food demand and quality, livestock and fibre production, energy use (fossil- and bio-fuel), and land use management. Owing to their large dimension, these human requirements are contributing to an unprecedented global change (e.g. climate, biogeochemical cycles, biodiversity).¹ As a result, by 2050 food demand is forecasted to double but the environmental footprint must be reduced to avoid major disruptions to the planet's processes and the collapse of modern civilization.¹ The problem is that the current increase in the use of fertilizers, water and arable land is both not sustainable¹ and is not keeping pace with the growing demand for food.² For instance, in the past half century, Chinese cereal grain yields increased 3.5-fold from 1.2 t ha⁻¹ to 5.4 t ha⁻¹, driven by a 5-fold increase in the use of chemical fertilizers.³ Given that agriculture is the main source of emissions of reduced forms of nitrogen (N), this significant increase in yield is responsible for the Chinese N deposition being now dominated by reduced forms of N, having increased from 13.2 kg N ha⁻¹ yr⁻¹ in the 1980s to 21.1 kg N ha⁻¹ yr⁻¹ in the 2000s.⁴ Another dramatic example of the consequences that long-term excessive use of fertilizers can have is the large dead zones formed in the Gulf of Mexico around the Mississippi delta.⁵

The concepts of soil health and quality were developed in response to environmental concerns regarding the excessive use of fertilizers. Soil health is defined as 'the ability of a soil to produce safe and nutritious crops in a sustained manner over the long term to enhance human and animal health without impairing the natural resource base or harming the environment'.⁶

In this context, a report of the Millennium Ecosystem Assessment⁷ acknowledged the essential role of soils for the benefit and welfare of humankind. Thus it seems obvious to put an emphasis on developing technological and ecological advances capable of enhancing soil health and filling the gap between productivity and sustainability in agriculture.

There is general consensus about the urgent need for more sustainable agricultural practices capable of generating higher crop yields. However, this is not likely to be achieved without multidisciplinary cooperation among (at least) soil science, agronomy, ecology, genetics, economics and social sciences and, of course, without the full engagement of farmers.⁸ This is important because, although agriculture sustains human population directly (i.e. quantity and quality of the food) and indirectly (e.g. fibre and biofuel production), it is a business where the main goal is to generate a profit. This means that farmers are not likely to implement novel agricultural practices to reduce the environmental footprint unless they add economic value to their business. This added value can simply be direct (e.g. reduction in costs with fertilizers, pesticides, irrigation or increased yield) or indirect (e.g. consumers' awareness of the

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environmental impacts of agriculture resulted in a ‘fork-to-farm’ movement where consumers, through their choices, influence how agriculture is practiced). Even though consumers’ options may appear to have little impact on everyday farm practices, they build up through social and economic movements. This is how market niches have been created and consolidated (e.g. organic farming, green commodities).

Looking back into the history of agriculture, crop rotations arose as one of the first sustainable agricultural practices.⁹ Crop rotations improve yields by taking advantage of niche complementarity, enabling the optimization of nutrient use and the reduction of pests and pathogen loads. With the arrival of the Green Revolution (i.e. heavy reliance on chemical fertilizers, pesticides, irrigation and improved and genetically modified crop varieties), the longer and more diverse crop rotations fell out of favour. This simplification of rotations had economic, environmental and social consequences. An example of social awareness to this topic is an opinion piece entitled ‘Did farmers of the past know more than we do?’, written by the American author Verlyn Klinkenberg.¹⁰ This piece reflected the author’s concerns about the way in which crop rotations have been simplified in the last 30 years in the Midwest region of the USA. They changed from 4-year rotations of oats mixed with alfalfa, clover, wheat, other small grains and turnips), to maize and soybeans alone. Klinkenberg¹⁰ argued that without the use of crop rotations the distribution of profit now favours agricultural-related industries (e.g. fertilizers, pesticides, seeds) and not the farmers. Finally, he highlights the importance of considering soil health to improve yield while lowering the environmental footprint. We propose that carefully (i.e. evidence-based) designed crop rotations combined with technologically advanced agricultural practices are an important avenue to attain food security and reduce the environmental footprint.

THE ADVANTAGES OF USING CROP ROTATIONS

A crop rotation corresponds to the successive cultivation of different crops in a specified order in the same field (Fig. 1). Crop rotation is considered a cornerstone of ‘integrated farming’,¹¹ being recommended by the Common Agricultural Program of the European Union.¹² According to Hazell and Norton,¹³ farmers have two main management options for implementing crop rotations: (i) they can either grow a single crop in the entire farm each season; or (ii) grow different crops concurrently each season either in different fields or in one field divided into parcels.

The interest in revisiting criteria used to design crop rotations and the factors associated with their productivity is especially timely due to the recognized beneficial outcomes in terms of soil health. Specifically, crop rotations contribute to: (i) breaking the dominance of weeds (e.g. crop rotations are recommended as a management practice against herbicide-resistant weeds) and the life cycles of host-specific herbivores and pathogens;^{14,15} (ii) improving soil structure through the development of different rooting systems that can more effectively exploit the soil, resulting in less soil compaction and degradation¹⁶ – in turn this leads to improved plant nutrition with increased carbon sequestration;¹⁷ (iii) enhancing soil quality as a result of the various crop residues that improve the quality of soil organic matter, particularly when leguminous plants are used; (iv) reducing soil erosion by at least 30% compared with intensive single-culture systems;¹⁸ (v) preventing groundwater pollution;¹¹ and (vi) contributing to landscape diversity,¹⁹ thus promoting biodiversity.²⁰ Taken

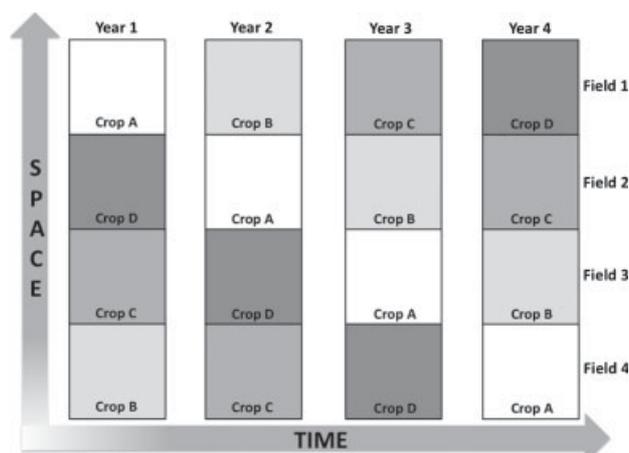


Figure 1. Schematic representation of a 4-year crop rotation. Depending on the size of the farm and on cropping management, crop rotations may involve only time or time and space.

together, this evidence supports that a diversified and carefully designed crop rotation (i.e. selection of crops based on site specificities) contributes to enhancing and stabilizing crop productivity and decreasing chemical inputs.

CURRENT CRITERIA FOR IMPLEMENTING CROP ROTATIONS

Many crops can be included into different crop rotations, making the number of possible combinations very high. Therefore, designing crop rotations must follow certain rules and criteria. In an attempt to find and compile these rules from the literature we started by searching the so-called grey literature (i.e. reports, farmers guidelines, etc.). We found a recent European research project report²¹ providing the most comprehensive list of rules and criteria, stating that optimal rotations should include:

- cash (e.g. maize) and soil-conserving cover crops (e.g. clover);
- deep-rooted (e.g. sweet clover, alfalfa) and shallow-rooted crops (e.g. cereals) to maximize nutrient availability along the soil profile;
- spring- and autumn-sown crops to break the life cycles of weeds, pests and pathogens;
- crops with a high level of ground cover (i.e. to maintain weeds at a low level) and those whose density allows weeds to be easily controlled mechanically;
- water-demanding crops (e.g. maize) and those that require less water (e.g. barley);
- crops that leave a large amount of plant residues after harvest;
- N₂-fixing legumes and high-N consumers (e.g. maize and winter wheat);
- more than one densely cultivated fast-growing crop (i.e. intercropping, cover crops or catch crops), as this maximizes nutrient use efficiency, reduces weeds through increased competition, protects soil structure, minimizing erosion, and provides different habitats for fauna, including beneficial insect pollinators.

Although these criteria were reported for Europe, the basic principles (i.e., reduction of soil erosion, maintenance or improvement of soil organic matter content, management of plant nutrition and control pests) can certainly apply to

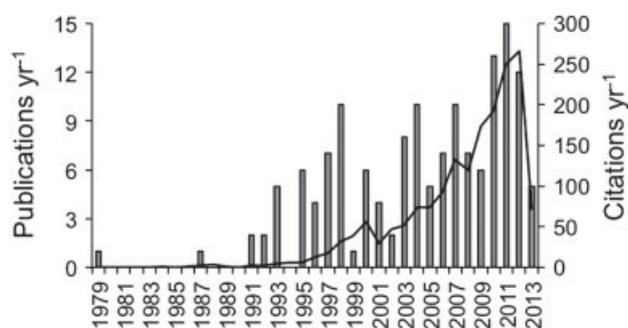


Figure 2. Distribution of Web of Science publications (bars) and their citations (line) per year. Web of Science was used to search the literature for empirical studies that tested and/or established the current criteria for designing crop rotations. Search topics consisted of 'criteria' AND 'crop rotation' from 1900 to 2013 and written in English.

other geographic areas and to both conventional and organic farming.

In our search of rules and criteria for crop rotations we then turned to the academic literature using Web of Science (Thomson Reuters, ON, Canada). Specifically searching for 'criteria' AND 'crop rotation' under 'topics', from 1900 to 2013 we found 149 publications (Fig. 2). The first publication was from 1979, but generally most publications on these topics were published in the last decade. However, after carefully reviewing all the papers obtained through our search we could not find a single one containing science-based criteria for crop rotations. Most publications did not focus on crop rotations *per se* but on management practices (e.g. tillage, fertilizations). The only publications that did contain some criteria for developing crop rotations focused on modelling. Why is the literature on this topic so scarce? Perhaps many rules and criteria for designing crop rotations are simply assumed to be well and long established among the farmers (after all, rotations have been common practice for millennia). Since the target audience of research on crop rotations is mainly the farmers, perhaps research on this topic is primarily published in textbooks, magazines, non-peer-reviewed journals or local journals that are not included in the Web of Science. Another possibility is that crop rotation research is very time consuming and therefore not appealing for developing research. It might also be that the rules and criteria for selecting crop rotations are indeed published in the scientific literature but hidden under different keywords (e.g. more specific studies on particular pathogens).

Designing crop rotations involves multiple and sometimes competing objectives (see review by Dury *et al.*²²): (i) socio-economic (e.g. maximizing profit while reducing equipment and labour costs); (ii) agronomic (e.g. maximization of irrigation area); and (iii) environmental (e.g. minimization of energy, nutrients and pesticide use and reduction of soil disturbance). As a result of the increasing complexity in crop management, many models have been developed in recent years. After reviewing 120 studies that specifically included cropping plan and crop rotation decision-making concepts into models, Dury *et al.*²² identified and grouped the parameters used to select a crop rotation as follows:

- predefined by expert;^{23,24}
- agronomic rules: considerations for timing, sequence, frequency and farm-specific constraints;^{25,26} forbidden²⁷ and allowed²⁸ crop sequences based on observation (i.e. criteria not scientifically tested as those listed above);²¹

- indicators of crop rotation quality: effects of a specific crop sequence (e.g. soil structure, diseases, pests, weeds and N), recurring crops and their respective recommended minimal return time and crop diversity;¹¹
- probability of crop occurrence: probability based on observed crop rotations;²⁹
- yield-reducing factors: regression analysis to estimate yield influence of preceding crop;³⁰ timing and sequencing constraints, disease classes associated with yield reduction penalties³¹ and predefined yield-reducing factors.²²

From the above, we can conclude that even with the application of modelling techniques expert judgment decisions are still required and many key criteria are not being considered. This is particularly evident when the objective is to meet multiple goals (economic, agronomic and environmental), as the attribution of a ranking system to each criterion introduces additional subjectivity.³² As a result, expert knowledge is often invoked to select a subset of rotations, which inherently increases the risk of overlooking potentially more effective alternatives.²⁵

Despite all the documented observational reports and expert knowledge on designing crop rotations, there appears to be no consistent scientific basis to justify the use of a particular crop rotation over another. In addition, as novel scientific advances become available (see sections below), other important criteria can, and should, be tested. For instance, the influence of plant–soil microbe interactions and soil–biota feedbacks on plant health and plant performance are well established for natural ecosystems, but this evidence is neither used nor is it acknowledged as a criterion for establishing crop rotations. The following sections explore how these biotic interactions can be used to optimize crop rotations.

THE CONTRIBUTION OF SOIL BIOTA TO NUTRIENT ACQUISITION

The productivity of most systems, including agricultural systems, is limited by the availability of phosphorus (P) and N. As such, understanding the role of plant–microbe interactions in governing the availability of these nutrients will enhance the economic and environmental sustainability of crop production.³³ In addition, most of the environmental problems associated with agriculture are linked to low nutrient use efficiency, especially of P and N, by the crops. In intensive agricultural systems nearly 50% of the applied fertilizer is lost,³⁴ posing serious environmental and economic constraints.³⁵ A more efficient use of P, with the consequent lower application of fertilizer, would reduce environmental damage, provide significant economic savings and reduce dependence on finite raw materials (rock phosphate) imported mainly from China, North Africa, Russia and the USA. Similarly, an efficient use of N would provide significant economic savings and reduce the energy burden necessary for the production of N fertilizers and environmental impacts due to N losses (e.g. leaching, surface run-off, denitrification and volatilization). Within the European Union alone, the impacts of the N losses have been estimated at €70–320 billion per year.³⁵ Selecting and improving crop varieties and managing associated soil microbial communities can enhance nutrient use efficiency.³³

Indeed, the contribution of soil microorganisms to P and N acquisition has been studied for natural and agricultural systems. For instance, van der Heijden *et al.*³⁶ showed that experimental plant communities inoculated with arbuscular mycorrhizal fungi (AMF; *Glomus* sp.) had on average 44% more P compared

with non-mycorrhizal plant communities, while N acquisition was only improved for some plant species (*Hieracium pilosella* and *Sanguisorba minor*). Mycorrhizal fungi and N₂-fixing bacteria are responsible for 5–20% (grassland and savannah) to 80% (temperate and boreal forests) of all N, and up to 75% of P, acquired by plants annually.³⁷

Regarding the microbial contribution to P and N acquisition by important crops, maize (*Zea mays*) plants inoculated with the AM fungus *Glomus mossae* were shown to receive at least 20% of the P from the fungal hyphae when compared to negative controls,³⁸ while sugar cane plants (*Saccharum* sp.) can receive 25–60% of N from the N₂-fixing bacteria.³⁹ The recognition for the large N input provided by the association between legume crops and N₂-fixing bacteria goes back to early farming.⁴⁰ The use of legume crops reduces the amount of N fertilizer for the legume's growth and for the subsequent crop in a rotation. Peterson and Russelle⁴¹ estimated that properly managed alfalfa–maize rotations in the upper Midwest of the USA could reduce fertilizer inputs by up to 25% without production losses, providing a realized net return of \$50–90 million yr⁻¹ in that region (assuming a fertilizer N price of \$0.22 kg⁻¹). Depending on management and cropping system, legume green manures (i.e. cover crops grown primarily to introduce nutrients and organic matter into the soil) have the potential to replace more than 100 kg N ha⁻¹ for a subsequent grain crop. This equates to savings of between \$60 and \$90 ha⁻¹ in N fertilizer. The enhanced yield due to the rotation effect coupled with the savings in fertilizer offset most potential losses that could arise as a result of lowering fertilizer inputs.⁴²

THE CONTRIBUTION OF SOIL BIOTA TO PLANT GROWTH

Several soil microorganisms promote plant growth, and new microbial products that stimulate plant growth are increasingly commercially available.⁴³ These microorganisms, called plant growth-promoting microorganisms (PGPMs), must be able to: (i) colonize a plant's root system; (ii) survive and multiply in microhabitats associated with the plant's root surface, at least for the time needed to express their benefits to the plant; and (iii) promote plant growth.^{44–47} PGP bacteria have been extensively studied for their capability to induce biomass production and systemic resistance to pathogens.⁴³ Conversely, by comparison with bacteria, PGP fungi such as those in the genera *Penicillium*, *Fusarium*, *Trichoderma* and *Phoma*, despite their recognized potential, have been largely neglected.⁴⁸ PGP bacteria can be endophytic or rhizospheric; they can enhance seed germination, root development, mineral nutrition and water utilization.^{49,50} The most studied feature of PGP fungi is protection against pathogens, which will be addressed in the following section. However, other features such as increased tolerance to drought, temperature, salinity or nutrient deficiency need more research.

PGPM benefits include production of plant hormones (auxins, cytokinins, gibberellins and ethylene);⁵¹ antagonism against phytopathogenic microorganisms and increased tolerance to micronutrient deficiency by production of siderophores⁵² and cyanide;⁵⁰ nutrient competition and induction of systemic host resistance; or enhancing the availability of minerals such as P.⁵² These benefits can be very specific to certain taxa. For instance, Montañez *et al.*⁵⁰ isolated 22 putative endophytic bacteria (*Rhanelia*, *Pantoea*, *Rhizobium*, *Pseudomonas*, *Herbaspirillum*, *Enterobacter*, *Brevundimonas* and *Burkholderia*) from maize plants

and characterized them for the presence of the *nifH* gene (N₂ fixation), auxin (IAA) and siderophore production and phosphate-solubilizing capacity. All the analysed strains produced IAA *in vitro* but only *Pseudomonas fluorescens* produced siderophores. The most frequent culturable N₂-fixing bacteria and the highest P solubilization capacity was provided by *Rhanelia* spp.

Despite their benefits for plant productivity, some PGPM species have been shown to affect human health. Therefore, their presence in the edible plant organs must be monitored and kept at safe values. *Pantoea agglomerans* is one such PGPM that improves the growth of maize plants,⁵³ but in humans causes infections in soft tissue or bone/joint.⁵⁴ Similarly, *Burkholderia* species have several applications (e.g. biological control of plant pathogens, bioremediation of recalcitrant xenobiotic compounds and plant growth promotion), but some *Burkholderia* species cause infections in humans.⁵⁵ Another aspect of this contrast between the benefits and drawbacks of using PGPMs is reported by Kikuchi *et al.*,⁵⁶ who demonstrated that the symbiosis established between some *Burkholderia* strains and a pest insect (stinkbugs, *Riptortus pedestris*) confers insecticide (fenitrothion) resistance to the host insects.

In summary, there is a very large number of PGPMs but their benefits depend on specific PGPM–plant combinations. Understanding these specificities should be a major goal of research that can lead to novel applications and adjustments to the design of crop rotations. In line with this goal, we suggest comparing the growth of important crops (e.g. maize, potato, tomato, soybean) in the presence of PGPMs isolated from different soils with or without various indigenous soil communities. The integration of these results on yield with data on how specifically rhizosphere biotic communities vary over time and under different management systems would contribute to laying the foundation for a much improved capacity to predict yields and provide novel microbial inoculants and indicators of soil health. We propose that these data should be widely available in open source databases (see sections below).

THE CONTRIBUTION OF SOIL BIOTA TO PROTECTION FROM PESTS AND PATHOGENS

There is a strong relationship between soil biota, soil fertility and plant health. The contribution of soil biota to plant pests and pathogen protection can occur through direct interactions with the plant (e.g. improved nutritional status or activation of the plant 'immune' system) or through other interactions within the rhizosphere (e.g. competition, predation and parasitism).^{57,58} The activity and effects of beneficial rhizosphere microorganisms on plant health are well documented for bacteria belonging to the Proteobacteria (noticeably *Pseudomonas* and *Burkholderia*) and Firmicutes (*Bacillus* and related genera), and for fungi from the Deuteromycetes (e.g. *Trichoderma*, *Gliocladium* and non-pathogenic *Fusarium oxysporum*).⁵⁹

Crops growing in nutrient-deficient soils are more susceptible to pests and disease attacks. For instance, maize infestation with the parasitic weed *Striga* sp. in N-deficient African soils was significantly reduced by increasing N availability using legume species as the previous cover crop.⁶⁰ Similarly, maize and sorghum infestation with *Striga hermonthica* was reduced by 30–50% after inoculation with AMF (*Glomus clarum* and *Gigaspora margarita*).⁶¹ Although this reduction in *S. hermonthica* infestation was largely due to

improved plant nutrition, interactions (e.g. competition for space, nutrients) within the rhizosphere could not be excluded.

In some cases it is difficult to separate soil biota effects on plant nutrition from those on plant physiology (e.g. hormones, secondary metabolites). For instance, inoculation of lima bean (*Phaseolus lunatus*) with rhizobia was shown to provide more N that was allocated both to plant growth and defence against herbivores (i.e. production of N-containing cyanogenic defence compounds). As a result, herbivory by the Mexican bean beetle (*Epilachna varivestis*) decreased significantly in the rhizobia-inoculated plants.⁶² Certain AMF defend their host plant against pathogen attacks^{63,64} even in situations in which AMF do not improve plant nutrition. Newsham *et al.*⁶⁵ inoculated seedlings of the annual grass *Vulpia ciliata* ssp. *ambigua* with a factorial combination of the cosmopolitan root pathogen *Fusarium oxysporum* and an AM fungus (*Glomus* sp. isolated from the study site). Under field conditions, plant growth or P concentration did not increase in AM-inoculated plants but fewer infections of pathogenic *F. oxysporum* developed. In addition, studies on the role of AM fungal diversity on plant pathogen or herbivore protection have provided evidence for certain AMF in the community acting as the main drivers of those effects, rather than diversity alone (i.e. a sampling effect).^{64–66}

Besides AMF, other fungi and bacteria have important roles in plant defence. For instance, *Trichoderma* spp. are free-living fungi that are highly interactive in roots, soil and leaves, producing a wide range of antibiotic substances and parasitizing other fungi.⁶⁷ They can also compete with other microorganisms for key exudates from seeds that stimulate the germination of propagules of plant-pathogenic fungi in the soil⁶⁸ and, more generally, compete with soil microorganisms for nutrients and space.⁶⁹ *Trichoderma* spp. also inhibit or degrade pectinases and other essential enzymes for plant-pathogenic fungi such as *Botrytis cinerea* to penetrate leaf surfaces.⁷⁰ In addition to the ability of *Trichoderma* spp. to attack or inhibit the growth of plant pathogens directly, they can also induce systemic and localized resistance to a variety of plant pathogens (for a review see Harman *et al.*⁶⁷). Similarly, *Burkholderia phytofirmans* strain PsJN is an endophyte that protects grapevine plants against the grey mould disease caused by *Botrytis cinerea*,⁷¹ but *Burkholderia andropogonis* causes bacterial stripe of sorghum and maize.⁷²

Management of soil biotic and abiotic properties is an important approach to promote the activities of beneficial microorganisms in the rhizosphere and to reduce soil-borne pathogens to a tolerable level.⁷³ Adaptation of agricultural practices has been proposed as a means of decreasing disease.⁷⁴ For instance, growing soybean after two or three cycles of maize reduced significantly (~50–90%, depending on soil type and other factors) the severity of *Sclerotinia* stem rot in soybean (caused by *Sclerotinia sclerotiorum*) when compared to growing soybean in monoculture.⁷⁵ Indeed, disease-suppressive soils have been generated through crop rotation, intercropping, residue destruction, organic amendments, tillage management practices and a combination of those regimes.⁵⁹

Based on the research reviewed in this paper, we consider that more important than aiming at soil microbial diversity *per se* is to identify the key microbes (including keystone species), or assemblages (consortia), that have a negative and positive influence on plant productivity. However, soil microbial communities vary widely in space and in time, adding uncertainty and complexity to the goal of identifying key species and consortia. To turn this information into predictors of soil health we suggest that soils should be sampled at the end of each crop cycle so that

positive and negative effects on productivity of the subsequent cycle could be screened and linked to the initial community (i.e. legacy effect). This way, farmers could, potentially, make use of this information and bioaugment the soil with crop- and soil-specific inoculants containing/promoting microorganisms that improve soil health. But this requires innovation through technology transfer to agricultural research. In the next section we will present our perspective on how this could be applied to crop rotations.

SOIL FEEDBACK EXPERIMENTS AND OTHER INNOVATIONS AT THE SERVICE OF AGRICULTURE

Plants exert abiotic and biotic effects (i.e. a conditioning or 'training' effect) on soil properties and processes, which in turn influence the growth, productivity and fitness of subsequent plants.⁷⁶ Plant–soil (a)biotic interactions that result in subsequent effects on plant growth and fitness are referred to as 'plant–soil feedback'.⁷⁷ Feedback can be neutral, positive or negative (i.e. a plant growing in soil conditioned by a previous plant can grow the same, more or less, respectively, relative to soil conditioned by different plant species). From a below-ground perspective the notion of plant–soil feedback laid the foundation for the design of crop rotations. Even the abundance and success of annual agricultural weeds is determined in part by plant–soil feedback mechanisms. In spite of this, the formal empirical testing of soil feedback by establishing a common garden experiment, including separating the biotic and abiotic soil-conditioning components, has, as far as we are aware, never been applied to inform the design of crop rotations. We consider that this represents a major gap in assessing soil health and establishing more sustainable crop rotations, and propose that plant–soil feedback should be assessed when designing crop rotations. Although this idea appears quite simple, the design of plant–soil feedback experiments is complex.⁷⁸ Feedback studies can focus on: (i) soil microbial feedback experiments that isolate the role of microbes in mediating plant–soil feedback through the use of conditioned soil inocula; and (ii) whole soil feedback experiments, which use a larger volume of conditioned soil and thus take into account feedback mediated by microbes as well as by any other plant-induced changes in soil properties.⁷⁶ We consider that the study of crop rotations should include both approaches simultaneously to disentangle the relative contribution of each crop to soil fertility as well as changes to the soil biota (Fig. 3). By doing this, it would be possible to assess whether effects of soil conditioning are indeed due to altered soil biotic community composition rather than to changes in nutrient status.

Despite the immense potential of soil feedback studies to being predictive in relation to crop rotations, the approach still consists of a 'black box' in that only plant growth responses are typically obtained without any insight about the factors that contributed to those responses. Recent developments in molecular microbiology, however, now offer immense potential to narrow the gap in the knowledge of biodiversity and determine more exactly the composition of soil microbial communities driving the growth of a certain subsequent crop. For instance second-generation sequencing methods such as 454 pyrosequencing allow the rapid analysis of millions of DNA sequence variations (i.e. single-nucleotide polymorphisms) in parallel without the need for Sanger sequencing. The use of this and other fast-developing second-generation sequencing technologies in

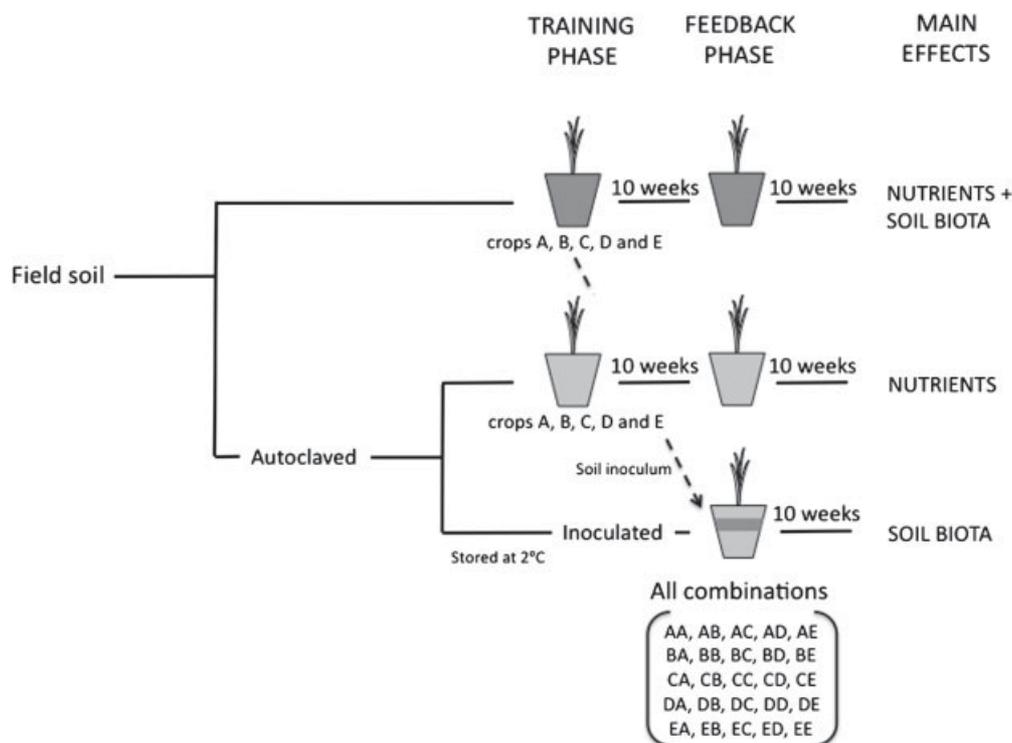


Figure 3. Schematic representation of a possible soil feedback experiment designed to disentangle the biotic and abiotic effects involved in crop rotations. Crops being considered for rotation are each grown in field soil, sterilized field soil and sterilized field soil inoculated with a fraction of field soil (as soil inoculum). Plants first condition the soil for a set period of 10 weeks. Subsequently, each crop is either grown on its own conditioned soil or in soil conditioned by each of the other crops.

conjunction with plant–soil feedback experiments as a tool to determine biotic diversity present in the roots and rhizospheric soil of important crops offers much potential to produce new databases for agriculture.⁷⁹ Such databases would be capable of better informing (e.g. through multivariate and network analysis, structured equation modelling) whether soil biotic communities contain key taxa or consortia that are conducive to crop productivity and soil health. This approach also has large potential toward the development of future targeted inoculants, i.e. contributing to the so-called high-precision agriculture.

CONCLUSIONS

Food production must increase substantially by 2050 and, concurrently, the environmental footprint must be reduced. The economic, agronomic and environmental benefits of crop rotations are well established. The contribution of soil biota to nutrient acquisition and plant growth and resistance to pests and pathogens is also well established. Currently, however, crops are selected and managed without considering the contribution of soil biota to yield and soil health. We propose that carefully (i.e. evidence-based) designed crop rotations that take into consideration plant–soil biota feedbacks and are further informed by soil biotic databases generated through the use of second-generation sequencing technologies can, in the near future, contribute to enhanced crop productivity and food security. Innovation (scientific and agricultural approaches and technologies) must be transferred and put at the service of agriculture. In addition, developing soil feedback studies and applying molecular identification methods towards the development of soil biotic community databases for the most

important crops can also serve to generate indicators of soil health and offers much potential toward the development of targeted inoculants.

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