

Chapter 10.

Using microbial community interactions within plant microbiomes to advance an evergreen agricultural revolution

M.E. Lucero¹, S. DeBolt², A. Unc³, A. Ruiz-Font⁴, L.V. Reyes⁵, R.L. McCulley⁶, S.C. Alderman⁷, R.D. Dinkins⁸, J.R. Barrow⁹ and D.A. Samac¹⁰

*End-O-Fite Enterprises LLC, 229 Vista Del Rey Drive, Vado, NM 88072, USA;*²*Department of Horticulture, University of Kentucky, N-318 Ag Sciences Center, Lexington, KY 40546, USA;*³*Boreal Ecosystems Research Initiative, Memorial University of Newfoundland, Grenfell Campus, Corner Brook, NL A2H 6P9, Canada;*⁴*Center for Applied Biotechnology Investigations, National Polytechnic Institute, Ex-Hacienda San Juan Molino, Carretera Tecuexcomac-Tepetitla, Lardizabal, Tlaxcala 90700, Mexico;*⁵*Graduate School, New Mexico State University, P.O. Box 30001 MSC 3-RRGS, Las Cruces, NM 88003, USA;*⁶*Department of Plant and Soil Sciences, University of Kentucky, 1405 Veterans Drive, Lexington, KY 40546, USA;*⁷*USDA-ARS, Forage, Seed, and Cereal Research Laboratory, 3450 Southwest Campus Way, Corvallis, OR 97331, USA;*⁸*USDA-ARS, Forage Animal Production Research Unit, 1100 S. Limestone, Lexington, KY 40503, USA;*⁹*USDA-ARS, Jornada Experimental Range, 2995 Knox Street, Las Cruces, NM 88003, USA;*¹⁰*USDA-ARS, Plant Science Research Unit, 1991 Upper Buford Circle, St. Paul, MN 55108, USA; malucero64@gmail.com*

Abstract

Innovative plant breeding and technology transfer fostered the Green Revolution (GR), which transformed agriculture worldwide by increasing grain yields in developing countries. The GR temporarily alleviated world hunger, but also reduced biodiversity, nutrient cycling, and carbon (C) sequestration that agricultural lands can provide. Meanwhile, economic disparity and food insecurity within and among countries continues. Subsequent agricultural advances, focused on objectives such as increasing crop yields or reducing the risk of a specific pest, have failed to meet food demands at the local scale or to restore lost ecosystem services. An increasing human population, climate change, growing per capita food and energy demands, and reduced ecosystem potential to provide agriculturally relevant services have created an unrelenting need for improved crop production practices. Meeting this need in a sustainable fashion will require interdisciplinary approaches that integrate plant and microbial ecology with efforts to advance crop production while mitigating effects of a changing climate. Metagenomic advances are revealing microbial dynamics that can simultaneously improve crop production and soil restoration while enhancing crop resistance to

environmental change. Restoring microbial diversity to contemporary agroecosystems could establish ecosystem services while reducing production costs for agricultural producers. Our framework for examining plant-microbial interactions at multiple scales, modeling outcomes to broadly explore potential impacts, and interacting with extension and training networks to transfer microbial based agricultural technologies across socioeconomic scales, offers an integrated strategy for advancing agroecosystem sustainability while minimizing potential for the kind of negative ecological and socioeconomic feedbacks that have resulted from many widely adopted agricultural technologies.

Keywords: appropriate technology, Green Revolution, metagenomics, microbial diversity, sustainable agriculture

10.1 Introduction

Innovations in plant genetics and agronomic practices from 1940 to 1970 launched the Green Revolution (GR), which increased crop production worldwide and accelerated development of industrialized agriculture (Ortiz *et al.*, 2007; Stanger and Lauer, 2008). The overall benefit of resulting agricultural practices and their impacts on both food security and environmental health have been debated for decades. The loss of microbial diversity associated with agroecosystems as a result of industrialized agricultural practices has not been a primary focus within this debate. Recently, advances in DNA sequencing of uncultured environmental samples (i.e. metagenomics) amplified awareness that complex microbial communities interact with plants to promote growth. New understanding of this interdependence between plants and microbiomes provides evidence that restoring microbial diversity to agroecosystems is crucial for mitigating impacts of climate change to achieve agricultural sustainability and food security.

In the discussion that follows, we will review GR outcomes and other components of industrialized agriculture that have reduced agroecosystem sustainability. We will highlight the complexities of agroecosystems which challenge contemporary efforts to increase food security and sustainability through improved crop production technologies. We will discuss the need to address this complexity with multidisciplinary efforts that consider impacts across varied spatial, temporal, and socioeconomic scales in order to develop diverse, appropriate technologies that make agriculture socially, economically, and environmentally sustainable. Finally, we will highlight the potential for microbe based technologies to contribute to such efforts in a manner that beneficially impacts both climate change mitigation and agroecosystem sustainability.

10.2 Green Revolution advancements decreased agroecosystem sustainability

Green Revolution technological advances resulted in plant genetic combinations that responded to chemical inputs with high yields. Implementation in Mexico transformed the country from a wheat-importing to a wheat-exporting nation. This prompted India, Pakistan, and Turkey to import Mexican wheat germplasms and technologies. Revolutionary success in these countries was attributed not only to the technical breakthroughs in plant nutrition and genetics, but also to the strategic coordination of social and economic factors. This coordinated effort, described as the kick-off strategy (Borlaug and Aresvik, 1973), was implemented in famine-threatened nations in the 1960's. Three components were involved:

1. distribution of selected wheat germplasms;
2. technology transfer via demonstration plots staged to make yield increases resulting from chemical fertilizers and hybrid grain cultivars visible to local producers, planners, government officials, and scientists;
3. government price supports that ensured profitability of the new practices.

India, Pakistan, and Turkey each saw wheat production double within five years after adapting Mexican wheat varieties (Ortiz *et al.*, 2007). The powerful beneficial impacts that ensued supported Norman Borlaug's Nobel Peace Prize in 1970, and contributed to a global transformation in agricultural practices.

Gains achieved through the GR inspired hope that technologies to increase crop yields would end, or at least reduce, world hunger. Unfortunately, this GR promise was not realized in a uniform or sustainable fashion. The failure to sustainably reduce hunger, despite increased production and continual technological advancement, can be attributed to a multitude of complex socioeconomic, political, and environmental factors that interact across scales and disciplines to negatively influence the geographic distribution of food and its utilization (Figure 10.1). Borlaug cited population growth and insufficient global understanding of crop production as factors that limited benefits through improved plant genetics. He lamented the limited disciplinary scope of agricultural research efforts in his time (Borlaug, 1977). M.S. Swaminathan, who was instrumental in bringing Borlaug's high yielding varieties to India, spent subsequent decades articulating the diverse ecosystem threats posed by narrowly focused efforts to increase crop yields.

The potential for temporal and spatial variation influencing food security, including economic disparity, human population growth, market demands, infrastructure, governmental policies, weather, climate, terrain, soil quality, genetic drift and pests, is high. This makes efforts to understand the consequences of technological changes

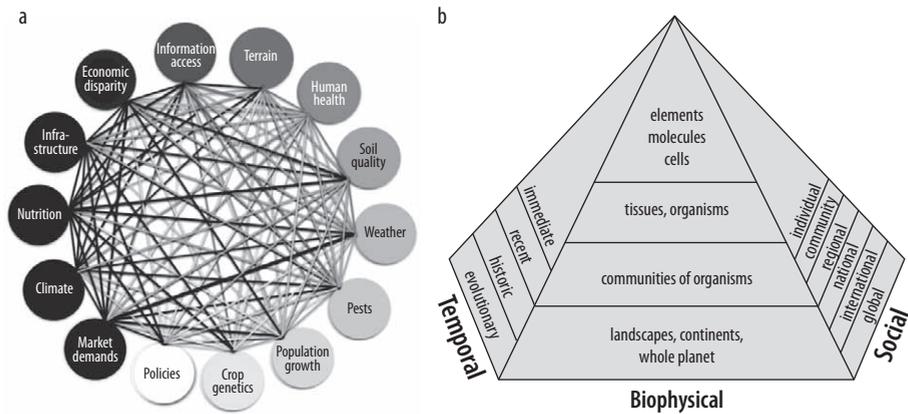


Figure 10.1. (a) Variables that interact to influence food security span infinitely complex disciplines and scales. Variables are selected from an infinite spectrum of interdependent factors that influence food security. Lines between variables illustrate potential for interactions that span spatial and temporal scales. (b) This subset of variables is broadly grouped into scaled temporal, biophysical, and social categories. Lines separating variables or groups of variables at each scale represent boundaries that can limit an individual's area of expertise.

tedious and costly to address (Figure 10.1a). Concerns that agricultural research is threatened by insufficient support for interdisciplinary research were articulated by agricultural scientists as early as the nineteenth century, when W.J. Spillman experimented with wheat genetics (Carlson, 2005). In order to document progress despite limited resources, it becomes tempting to achieve advancement or impact in narrowly focused areas deemed important by many (e.g. crop yields). However, this approach fails to address the significance of those interacting factors that are more difficult to control, such as climate change, insect and microbial populations, human understanding of ecology and economics. Hence, scientists frequently specialize in relatively narrow areas of expertise that span a minimal number of disciplines and scales (Figure 10.1b).

The GR provides an illustration of the potential for interacting factors to create long-term problems when technological breakthroughs in a few areas, including plant genetics, mechanization, and the development of chemical fertilizers, are broadly implemented. Green Revolution technologies clearly allowed growers to temporarily increase crop yields on depleted soils. The dire threat of famine at the time prompted complementary efforts in international diplomacy, extension, and government intervention that evaded famine and expanded the global reach of industrialized agriculture. The need for rapid decision-making outweighed the need for careful,

long-term planning. Unfortunately, after famine was evaded, GR practices were widely adopted at the expense of developing long-term soil building practices. This occurred despite concerns expressed by GR leaders that widespread adoption could lead to an era of agricultural disaster (Swaminathan, 1968).

Today, our global population includes nearly 1 billion humans who suffer from chronic hunger (FAO, 2008), and others who suffer from malnutrition. Meanwhile, soil erosion, reduced soil and water quality, and lost biodiversity associated with contemporary agricultural practices is high (Gunningham, 2007; Kiers *et al.*, 2008). The challenge we face is to devise new agricultural approaches that consider not only improved crop yield and hardiness under controlled management conditions, but also the broader, less manageable ecological and socioeconomic factors that interact across scales to influence food security and environmental quality. To meet this challenge, we must recognize the full complexity of the problem.

Figure 10.1a illustrates the arguably infinite spectrum of interdependent variables that interact to influence food security. Due to their intrinsic interconnectedness, manipulation of any set of variables will have direct or indirect, immediate or deferred influences on other variables. For example, a manager's access to information about pest populations may prompt decisions to treat crops with insecticide. The decision may be driven by the real need to manage income. However, the action will also impact soil and water quality, biodiversity, human health, nutrition, and other variables in ways that are more difficult to evaluate.

Scaling of variables is illustrated in Figure 10.1b, and interactions across scales must also be considered in order to better understand the potential for decisions to manage a set of variables at one scale, such as altered amino acid biosynthetic pathways engineered into a plant genome at the molecular scale, to influence other variables including microbial interactions, crop production costs, human nutrition, public perception, at other scales. Hence, managers, researchers and policy makers addressing food security are faced with the task of assessing limitless potential outcomes with finite resources.

10.3 Multi-scaled and multidisciplinary efforts help ensure sustainability

To truly make agricultural advances that benefit society as a whole, it is important to integrate an understanding of those technologies developed within one discipline, and applied at a single scale. This includes advances that enhance cellular communication between plant roots and rhizobia, with the broader, less tangible effects that these variables may have on related factors at broader scales such as pest populations, human nutrition, and environmental quality. In addition to these broader impacts, we must

also acknowledge that GR technologies, which were implemented to alleviate hunger by increasing crop production, are recognized by many to have confounded issues by supporting population growth, loss of small farms, environmental degradation, and calorie rich, nutrient poor dietary practices (Das, 2002; Lairon, 2010; Pinstруп-Anderson and Hazell, 1985).

With an increasing human population, industrial development also progresses. Climate change and environmental degradation ensue, which challenge sustainable crop production (FAO, 2008; Sanchez and Swaminathan, 2005; Swaminathan, 2010; UN Millennium Project, 2005). For example, climate change has the potential to increase the abiotic stress on crops while altering the environmental niches for pests, pathogens, and weeds. Alternately, enhancing food production using current technologies increases fuel requirements, but depleted fuel reserves drive demand for biofuels, making crop production for food and fuel directly competitive. Each of these concerns is closely tied to parallel concerns with environmental quality.

Numerous local, regional, and global efforts are currently addressing food security with innovative information and technology transfer efforts (Bill and Melinda Gates Foundation, 2009; FAO, 2011; Lombard *et al.*, 2006; Ortiz, 2006; Ortiz *et al.*, 2007). The term Evergreen Revolution (ER) was coined to articulate the need for making the outcomes of these efforts sustainable (Swaminathan, 2010). It is uncertain whether contemporary approaches, which are all important ER building blocks, will be adequate to address current and future food demands (Sanchez and Swaminathan, 2005). Notably, the majority of these efforts remain phytocentric, emphasizing plant-based technologies for enhancing crop production (Lynch, 2007; Ortiz *et al.*, 2007).

Recent advances in understanding plant-microbe interactions, driven by new technologies that allow the rapid assessment of microbial communities, hold significant promise for meeting global needs to accelerate the ER. In this chapter, we highlight the untapped potential of microbial communities to improve crop yields while restoring soil building, nutrient cycling, and pest reduction properties to agroecosystems. We note features of microbe assisted plant production that offer socioeconomic benefits for small farmers and carbon (C) sequestration features that offer relevance for mitigating the impacts of climate change. We also describe a fundamental strategy that can accelerate understanding of plant-microbe interactions within the multi-scaled context of entire agroecosystems. We outline existing and developing networks designed to promote information sharing and participatory research to extend new knowledge across socioeconomic and geographic scales. We end by summarizing the critical need for policies that promote this and other broad, integrated, and long term efforts to advance sustainable agriculture and related food security.

10.4 Microbial interactions across plant, soil, and environmental interfaces

In undisturbed ecosystems, plants are associated with a continuum of other organisms, the majority of which are microbial. These include epiphytes on plant surfaces, endophytes within plants, and rhizosphere and soil microbes associated with subsurface plant organs and soil interfaces (Figure 10.2). These microbiomes sequester significant amounts of atmospheric C, thus aiding in mitigation of climate change (Müller-Stöver *et al.*, 2012). Furthermore, microbiomes connect plants to surrounding substrates (Green *et al.*, 2008; Khidir *et al.*, 2008), cycle nutrients (Barrow *et al.*, 2008; Green *et al.*, 2008; Rodriguez and Fraga, 1999) stabilize soil (Gale *et al.*, 2000); enhance tolerance to biotic and abiotic stress (Barrow *et al.*, 2008), and buffer the impact of environmental factors on plants (Gale *et al.*, 2000; Lee *et al.*, 2009; Okon, 1985; Plett and Martin, 2011; Rodriguez and Fraga, 1999; Rodriguez and Redman, 2008). Remarkably, these microbial functions parallel many of the management actions humans perform to enhance crop growth in agroecosystems (Barrow *et al.*, 2008). For example, microbes can produce alkaloids that deter insect pests, reducing the need for applied pesticides (Kuldau and Bacon, 2008; Schardl *et al.*, 2004). Microbes fix atmospheric nitrogen, and solubilize phosphorus, which can replace the need for mineral fertilizer (Richardson, 2001; Rodriguez and Fraga, 1999; Stanger and Lauer, 2008). Microbes improve soil aggregation, increasing both soil aeration and soil water holding capacity (Gale *et al.*, 2000) in ways that may reduce the need for intensive irrigation management or deep ploughing.

Notably, while much crop research is devoted to the study of mycorrhizal fungi, rhizobia, and other root-associated microbes that fix nitrogen, endophytes (Barrow *et al.*, 2008) and soil crust microbes (Briggs and Morgan, 2012; Evans and Belnap, 1999; Green *et al.*, 2008) have been most heavily studied in pasture grasses and natural ecosystems. Endophytes are of growing interest to agriculture because the benefits they confer to plants may be transferred across generations, offering a rapid, inexpensive alternative to genetic engineering (Barrow *et al.*, 2008). Soil crust microbes, which have the capacity to fix nitrogen and promote soil stability (Briggs and Morgan, 2012; Evans and Belnap, 1999), are largely ignored in agroecosystems. Industrial agricultural practices such as mechanical planting, tilling and cultivation, application of synthetic fertilizers and pesticides, and harvesting disturb structural integrity and functional diversity of associated microbial communities, forcing increased reliance on artificial inputs to maintain crop yields.

Historically, advances that increased agricultural production were achieved largely through bypassing plant-microbiome associations, relying instead on tillage to manage weeds and soil compaction, and agrochemicals to provide nutrients and to remove

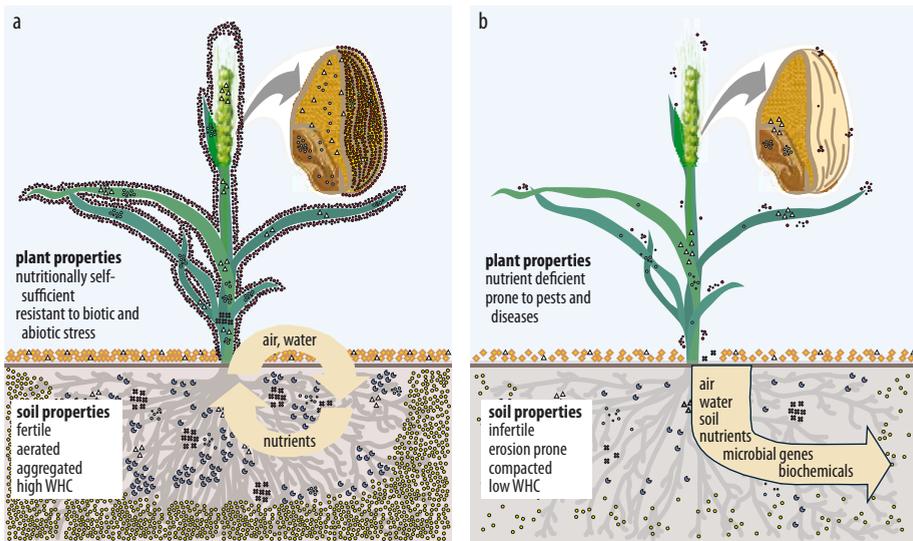


Figure 10.2. (a) Plants in undisturbed ecosystems interact with a continuum of microbial endophytes (light grey circles illustrated in plant tissues) and epiphytes (dark grey circles illustrated on plant surfaces), rhizosphere microbes (black outlined grey crescents illustrated on and near plant roots), soil crust microbes (dark grey outlined grey diamonds illustrated on soil surface), facultative (grey outlined white triangles illustrated in and on plants and soil), and free living soil microbes (black outlined light grey circles illustrated in soil) that interact to cycle basic nutrients and/or respond to biotic and abiotic stress. Microbes build valuable soil properties including aggregation, aeration, and water holding capacity (WHC). (b) In conventional agroecosystems, microbial communities may be altered and/or reduced by fertilization, fumigation or application of broad spectrum pesticides. These practices can deplete nutrients, decrease stress tolerance, and leave soil erosion-prone and compacted, reducing ecosystem capacity to sequester atmospheric carbon. Resulting crops may also differ in genetic, biochemical, and/or nutritional quality.

biotic stressors. Such an approach was unavoidable, because until recently, microbial communities and their associated effects on plant physiology could not be efficiently detected or studied. Bypassing the role of microbes and other plant-supporting biota resulted in the implementation of practices, such as application of non-selective pesticides to reduce pathogens, which unintentionally decoupled plants from their supporting organisms, including those vast microbial communities whose co-evolutionary success mandated efficient synchronization of plant primary production with decomposition, nutrient solubilization, and soil formation processes.

Many contemporary agronomic practices and agrochemicals negatively influence microbial community structures, adversely impacting soil fertility (Bueno and Ladha,

2009; Fox *et al.*, 2007) and C emissions (Dubey and Lal, 2009), while contributing to environmental degradation (Kiers *et al.*, 2008). As environmental impacts associated with these actions, including reduced C sequestration, loss of beneficial insect populations, increased soil erosion, and groundwater contamination by agrochemicals are recognized, the actions themselves have been justified by our critical need to feed the expanding human population. This justification persists despite awareness that the practices themselves negatively impact the input costs associated with crop production, making food security increasingly difficult for low income communities to attain (Kiers *et al.*, 2008).

10.5 Evaluating microbial potential to revolutionize agroecosystem sustainability

An alternative to advancing food security and mitigating climate change through phytocentric agricultural technologies is to leverage entire microbial communities to cycle nutrients, build soil aggregates, and boost plant stress tolerance (Barrow *et al.*, 2008; Dubey and Lal, 2009; Rodriguez and Redman, 2008). Potential benefits of exploiting microbial interactions with plants have been recognized for well over a century (Frank, 2005). Indeed, some of these benefits have already been adopted through improved crop rotation, precision farming, and organic farming, reduced tillage, and integrated pest management (Dubey and Lal, 2009; Stanger and Lauer, 2008; Swaminathan, 2010). Introducing nitrogen-fixing or phosphorus-mobilizing microbes into crop production systems can increase nutrient availability (Rodriguez and Fraga, 1999; Stanger and Lauer, 2008). For example, transfer of seed-borne endophytic microbes may create new germplasms with improved stress tolerance (Barrow *et al.*, 2008).

To date, outcomes to harness microbial services vary. Such variation is attributed to insufficient understanding of the complexity of microbial communities, lack of genetic compatibility between tested hosts and microbes, and poor microbial detection and monitoring technologies (Barrow *et al.*, 2008; Richardson, 2001). New high throughput DNA sequencing approaches offer the first significantly feasible opportunities to broadly examine those microbial interactions important for increasing plant production (Committee on Metagenomics, 2007). These techniques, including metagenomics to describe microbial community genetic diversity, and transcriptomics, proteomics or metabolomics to describe molecular scale community interactions are now applied to plant and soil microbial systems to explore microbial influences on sustainable plant productivity.

Even the most advanced, high throughput methods available today fail to detect large portions of the microbial communities present (Lucero *et al.*, 2011), and it is unlikely

that the incredible diversity of microbial kingdoms will never be entirely understood. This is one reason why an approach that utilizes knowledge of biotic patterns and processes observed at larger scales may aid in understanding microbial process at fine scales which may leverage crop production.

While it will never be possible to assess all the variables that could interact within an agroecosystem, these complex and cross-scale interactions can be better understood through networked efforts that combine data from diverse ecosystem components, and simulation models for multiple, linked scales (Peters *et al.*, 2007). Such networked efforts enable specialists within highly focused areas of expertise such as genomics, microbial ecology, soil science and economics, to consider broader suites of drivers and responses, including immediate and latent responses to management actions. Such a networked approach to address complex ecological questions has already been established (Moran *et al.*, 2008; Peters *et al.*, 2004, 2007).

A conceptual framework relevant for advancing sustainable, microbial based agroecosystems to enhance food security and mitigate climate change could include a synthesis of ecological data collected from fine to broad spatial and temporal scales, and socioeconomic data collected from diverse populations, as detailed below. Such data, much of which is already available through unrelated analyses carried out across varied natural science disciplines, could be linked through simulation models that illustrate immediate and long term effects of management actions on microbial community assemblages and agroecosystem function. These linked models may be useful for predicting immediate and long-term consequences of management actions with varied impacts on microbial community structures, allowing the exploration of risks and benefits of new technologies before their implementation.

Elemental, cellular, and molecular scale

Experts in chemistry, molecular biology, and biochemistry could further contribute to our understanding of interactions that occur at very fine scales, including nutrient cycling and microbial community structure and function. Genetic and metabolic differences between microbial communities can be revealed through nucleic acid sequencing or metabolic profiling (Committee on Metagenomics, 2007; Lucero *et al.*, 2011). Whole genome sequencing, proteomics, and/or metabolomics of bacteria and fungi associated with plants may advance our understanding of microbial functions that influence plant production, drought and salinity tolerance, chemical defense, growth, pathogenesis, nutrient cycling, primary and secondary metabolism, and nutrition. Microbial genomes deemed valuable for germplasm development may be sequenced to evaluate genes regulating host specificity, biotic and abiotic stress tolerance, pathogenesis, and

secondary metabolism (Kuldau and Bacon, 2008; Schardl *et al.*, 2004). Metagenomes (genomic sequences of entire microbial communities) associated with a plant host in a selected habitat may reveal the complete metabolic potential of microbiomes to influence crop production and other kinds of C sequestration, including the rates of C fixation and biomineralization catalysed by soil microbes. Databases such as the National Center for Biotechnology Information (Genbank) or Cyberinfrastructure for Advanced Microbial Ecology Research and Analysis (CAMERA) already provide publicly available collections of ecological and metagenomic data that, in combination with related research papers can provide foundational information for fine scale simulation models. When linked to simulations carried out at larger scales, these models can be used to forecast how microbial communities might respond to selected management actions such as soil tillage or irrigation, and to understand how these microbial responses might influence factors observed at larger scales including global C sequestration.

Tissue and whole plant scale

Plant physiologists, plant breeders, and microbial ecologists may interact to explore variations in microbiomes associated with native plants and crop plants of varied domestication histories to further understand how management practices impact plant associated microbial communities. In addition, microbial interactions that influence plant productivity and nutrient content may be evaluated. Tag encoded pyrosequencing of microbial communities associated with host plants and surrounding soils can be utilized in conjunction with plant performance bioassays to assess microbial community composition associated with variations in plant production parameters. Laboratory, greenhouse, and field bioassays in which microbial communities are manipulated by adding or removing specific groups of microbes can reveal conditions wherein microbes interact with host plants and/or with other plant associated microbes. Experiments across drought or other environmental stress gradients can reveal mechanisms by which microbes relate to whole plant stress responses that influence crop production. Simulated crop production forecasts may be fed into fine scale models to demonstrate how these vegetative changes might influence C and nitrogen cycling within the soil microbial community. Outputs from both linked simulations can be used as variables in global scale simulations.

Community or biome scale

Microbial communities associated with seeds, leaves, roots, and soil associated with specific cropping systems including conventional monocultures, rotated crops and no-till systems, can be examined to understand how microbial dynamics are influenced

by plant community composition. Combining such analyses with comparisons of microbial persistence across trophic levels could reveal microbe-plant interactions with the potential to propagate across food chains. Analyses of microbes associated with neighboring and invasive plants may provide insights into community interactions important for resisting pest invasion, with implications for both crop production and environmental restoration. The resulting ability to predict which cropping systems will be most resistant to invasions or other environmental threats will facilitate planning that ensures productivity even when climatic change makes historic practices obsolete.

Parameters influencing patch scale soil characteristics are already extensively documented at many national scales. For example, soil map units and related ecological site descriptions are publicly available through the USDA Natural Resource Conservation Service (USDA-NRCS). The ambitious, global scale ISRIC World Soil Information Database strives to meet growing global demands by making spatially related data describing soil, climate, geomorphology, vegetation, land use, and other variables available worldwide. By documenting spatial coordinates and describing the ecological parameters associated with field sample locations, these existing, detailed, and publicly available long-term datasets may be leveraged to understand habitat parameters that influence crop production.

Landscape to global scale

Geospatial coordinates and ecological site descriptions associated with each environmental sample could facilitate cross-site comparisons and reveal distinct habitat and management variables that influence microbiome compositions across geographic scales. Such analyses can be powerful for understanding the soil, landscape, and climatic factors influencing crop responses to microbial modifications, and for understanding how these responses might differ as habitats change. Phylogeographic analyses across regional to global scales can be applied to exploring the role of temporal, climatic, and edaphic factors on plant and microbial adaptation, community structure, and co-evolution. Disentangling effects of different factors can best be achieved through these geographic scale analyses where multiple factors can be examined separately and in combination. Linking these broad scale factors, like climate variables or landscape effects, to simulation models predicting crop productivity can aid land managers in the development of locally relevant management practices.

Dynamics that vary across temporal scales

The enormous genetic diversity of microbiomes and their short generation times allows rapid and dynamic response to environmental change. Changes in microbial

community structure following seasonal changes or management activities are expected. Using these changes to benefit production or buffer agroecosystem responses to climate change will require further understanding of the temporal dynamics of microbial responses to environmental drivers. Endophyte associations, which may transcend plant generations or influence host ecology, can best be understood through evolutionary analyses of host plants and associated microbes. Such studies, carried out in conjunction with phylogenetic analyses of genetically related plants, could provide transformational insights into how microbes influence plant adaptation. Phylogenetic comparisons that evaluate microbes associated with native, heirloom, and commercial plant germplasms will be uniquely valuable for illustrating important associations that have been lost as a result of various domestication, breeding, and selection practices (Couch *et al.*, 2005; Doebley *et al.*, 2006; Eyre-Walker *et al.*, 1998).

A hierarchy in temporal scales roughly corresponds to the spatial scales described above. While microbial communities can respond rapidly to climate drivers or management, with dominant taxa shifting over periods of minutes to days, dominant taxa in plant communities may take weeks, months, or even years to change. Insights from these spatial and temporal interactions suggested that rapidly responding microbial communities may assist plants in adapting to climate change more rapidly than may be expected through plant genetic change alone. Experiments that test these insights will be valuable for devising strategies that enhance plant production or that make plant communities resilient to climate change.

Management across socioeconomic scales

In agroecosystems, crops are influenced not only by standard biophysical parameters such as climate, soil, and wildlife, but also by human management decisions and actions. Humans decide what crop species to plant, where to plant them, and how to alter the natural environment in order to support crop plants. Such decisions are largely information driven, because they are based on our understanding of how biophysical parameters influence plant productivity and interact over time with various factors including production costs, market prices, labor, consumer tastes and preferences. Like biophysical and temporal parameters, socioeconomic parameters interact across scales. Hence, an individual crop producer's decision to grow a specific crop might be influenced at the national level by information about government price incentives and at the local or regional level by knowledge of consumer demand, production capacity, and marketing networks. Such information driven human management decisions are among the most powerful determinants of food security, climate change mitigation, and agroecosystem sustainability. For this reason, it is important that managers

have sufficient information, resources, and decision making authority to implement practices that are adapted to the conditions influencing their local environment.

Models and experiences that illustrate the complex, cross-scale interactions impacting people and environments whenever new management approaches are introduced will be helpful to evaluate management decisions prior to their implementation. Making such illustrations widely available, while reducing broad policies that limit management and purchasing options, will empower individuals to explore immediate and long-term consequences of varied actions, thus learning from a combination of real and simulated experiences. This will allow producers and consumers to make informed decisions that effectively balance short-term financial and caloric needs with locally adapted strategies that promote long-term human health and environmental integrity.

Global advances in educational and information technology, including the widespread availability of internet services and cell phone applications promise opportunity to make such models and tools broadly available to diverse socioeconomic strata (Bill and Melinda Gates Foundation, 2009; Sanchez and Swaminathan, 2005; Swaminathan, 2010). Modernized kick-off strategies will need to fully utilize these advancements while simultaneously increasing time honoured extension and education efforts, in order to promote effective information transfer to policy makers, crop producers, food processors, distributors, and consumers.

Information access across socioeconomic scales

The need for data accessibility to broad sectors of public users cannot be understated. Insufficient community level understanding of environmental and nutritional dynamics behind food production technologies could lead to an exacerbation of existing socioeconomic disparity (FAO, 2011; Sanchez and Swaminathan, 2005; Swaminathan, 2010). If the goal of an ER is to achieve sustainable agroecosystems, it is critical that research and the development of new agricultural and food technologies be accompanied by aggressive, innovative efforts to share our understanding of food production technologies and their potential environmental effects. The collective understanding of such efforts must include not only understanding of how to increase crop yields or nutritional values, but also understanding of how different management practices and consumer choices influence ecosystem services that are crucial for the long-term sustainability of agroecosystem management practices. This task can be made manageable by including producers, educators, market developers, policy makers, and consumers in various aspects of planning and implementing agricultural, research and technology transfer efforts. Models such as those embraced by non-profit groups like the International Centers for Appropriate Technology and Indigenous Sustainability

(iCATIS), illustrate how these difficult efforts may be advanced through networked partnerships.

10.6 Microbial potential to advance food security and mitigate climate change

Agricultural practices that promote integrated, functional plant and soil microbiomes are expected to promote plant and soil quality in manners that sustain, or even increase crop yields while mitigating the impacts of climate change. Organic farming protocols represent steps in the right direction, because they reduce the chemical disruption of plant and soil microbiomes. However, such protocols do not necessarily reduce mechanical disruption or promote microbial community development sufficiently to foster microbial communities that effectively manage soil moisture and cycle C, nitrogen, and other nutrients. Efforts that evaluate crop yields in conjunction with management practices and microbial community structure are needed. Such efforts are expected to reveal existing practices that simultaneously foster high crop yields, low input costs, and improved ecosystem services. Such practices are likely to vary across agroecosystems, because microbial communities that thrive in one habitat will not be optimal in other habitats.

This natural variation in adapted soil microbial communities and the resulting need for variation in management practices could theoretically provide positive socioeconomic feedbacks by increasing demand for local agricultural experts and improve opportunities for small, diversified farms. The resulting shift from agricultural leadership and expertise provided by broad scale government and corporate entities towards leadership within local communities may foster more direct interactions between growers and consumers. These interactions can improve food security at the community level by promoting diversified food systems that are more responsive to culturally and environmentally diverse demands. Benefits may be particularly significant within indigenous communities, where ancient and locally preserved cultural practices may hold critical clues to develop sustainable technologies that restore microbial diversity to local and regional agroecosystems. Communities that have retained these geographically specific knowledge bases will be well-positioned to initiate new commercial practices that involve training local growers to produce food without agrochemicals, sell climatically adapted heirloom seeds, and develop smallscale technologies for processing regionally unique food types. Such foods are already sought by a new generation of consumers that is increasingly interested in organic and locally grown foods.

10.7 Conclusions

Historic efforts to promote sustainable agroecosystem management practices have demonstrated that increasing plant production without attention to ecological and social impacts is devastating to long-term agroecosystem stability and food security. New breakthroughs revealing the complexity and importance of plant microbiomes offer exciting potential for developing management practices that promote sustainable food security and mitigate climate change. Practices that foster quality plant microbiomes could substitute biotic interactions that enhance crop fitness and yields while restoring soil quality and nutrient cycling functions, including C sequestration. Properly developed soil microbial communities may eliminate the need for mineral fertilizers. Plants colonized by drought tolerant, nitrogen fixing and halophytic microbial consortia may produce crops in arid or saline soils. Restoring endophytic microbes may enhance crop nutritional value by adding metabolic pathways that supplement the vitamins, proteins, and antioxidants produced by their host plants. Because microbial community composition can change rapidly in response to environmental change, microbial associations also lend metabolic plasticity to plant hosts, facilitating adaptation to climate change.

Breakthroughs in communication and information transfer will help ensure that new microbial technologies are implemented in ways that minimize undesired environmental impacts. Global databases increasingly facilitate developing models that illustrate the multi-scaled interactions between plants, microbes, humans, and changing environments. Such robust, multi-scaled models will enable users to thoroughly assess benefits and risks associated with new crop technologies. These models should help prevent the kinds of unintended consequences of the GR. For this reason, multi-scaled ecological models, in combination with new microbial technologies, could accelerate global progress towards food security and sustainable agriculture. This is particularly true if both are made accessible through networked, interdisciplinary, and participatory efforts that promote our understanding of biotic interactions across biophysical, temporal, and socioeconomic scales. These endeavours should be synergistic with existing efforts to address food security.

A well-informed public is crucial to success of any such effort. Public participation can minimize the potential for widespread negative ecological and socioeconomic feedbacks that could stem from newly developed agricultural technologies. It is of great importance for agricultural producers, policymakers, researchers, and educators to review time honoured concepts of education and extension as equalizers of socioeconomic disparity and as cornerstones to sustainable development (UN Millennium Project Task Force on Science, Technology, and Innovation, 2005; Mann, 1848; Peters 2006). Policies

and practices that support integration of microbial ecology with crop development, agroecology, environmental sciences, nutrition, socioeconomics, and extension will promote robust, adaptable, and sustainable agroecosystems with the improved potential to mitigate impacts of globalization and climate change.

References

- Barrow, J.R., Lucero, M.E., Reyes-Vera, I. and Havstad, K., 2008. Do symbiotic microbes have a role in plant evolution, performance and response to stress? *Communicative and Integrative Biology* 1: 69-93.
- Bill and Melinda Gates Foundation, 2009. Global development program fact sheet, Bill & Melinda Gates Foundation. Available at: <http://www.gatesfoundation.org/about/Documents/GlobalDevelopmentProgramFactSheet.pdf>.
- Borlaug, N.E., 1977. The green revolution: can we make it meet expectations? *Proceedings of the American Phytopathological Society* 3: 6-21.
- Borlaug, N.E. and Aresvik, O.H., 1973. The green revolution-an approach to agricultural development and some of its economic implications. *International Journal of Agrarian Affairs* 4: 385-402.
- Briggs, A.L. and Morgan, J.W., 2012. Post-cultivation recovery of biological soil crusts in semi-arid native grasslands, southern Australia. *Journal of Arid Environments* 77: 84-89.
- Bueno, C.S. and Ladha, J.K., 2009. Comparison of soil properties between continuously cultivated and adjacent uncultivated soils in rice-based systems. *Biology and Fertility of Soils* 45: 499-509.
- Carlson, L., 2005. Forging his own path: William Jasper Spillman and progressive era breeding and genetics. *Agricultural History* 79: 50-73.
- Committee on Metagenomics: challenges and functional applications, National Research Council, 2007. *The new science of metagenomics: revealing the secrets of our microbial planet*. The National Academies Press, Washington, DC, USA. Available at: http://www.nap.edu/openbook.php?record_id=11902.
- Couch, B.C., Fudal, I., Lebrun, M.H., Tharreau, D., Valent, B., Van Kim, P., Nottéghem, J.L. and Kohn, L.M., 2005. Origins of host-specific populations of the blast pathogen *Magnaporthe oryzae* in crop domestication with subsequent expansion of pandemic clones on rice and weeds of rice. *Genetics* 170: 613-630.
- Das, R.J., 2002. The green revolution and poverty: a theoretical and empirical examination of the relation between technology and society. *Geoforum* 33: 55-72.
- Doebley, J., Gaut, B. and Smith, B., 2006. The molecular genetics of crop domestication. *Cell* 127: 1309-1321.
- Dubey, A. and Lal, R., 2009. Carbon footprint and sustainability of agricultural production systems in Punjab, India, and Ohio, USA. *Journal of Crop Improvement* 23: 332-350.
- Evans, R.D. and Belnap, J., 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology* 80: 150-160.

- Eyre-Walker, A., Gaut, R.L., Hilton, H., Feldman, D.L. and Gaut, B.S., 1998. Investigation of the bottleneck leading to the domestication of maize. *Proceedings of the National Academy of Sciences of the USA* 95: 4441-4446.
- Food and Agriculture Organization (FAO), 2008. High food prices and food security-threats and opportunities, Food and Agriculture Organization of the United Nations, Rome, Italy. Available at: <ftp://ftp.fao.org/docrep/fao/011/i0291e/i0291e00.pdf>.
- Food and Agriculture Organization (FAO), 2011. How does international price volatility affect domestic economies and food security? Food and Agriculture Organization of the United Nations, Rome, Italy. Available at: <http://www.fao.org/docrep/013/i2050e/i2050e.pdf>.
- Fox, J.E., Burow, M.E., McLachlan, J.A., Gullede, J. and Engelhaupt, E., 2007. Pesticides reduce symbiotic efficiency of nitrogen-fixing rhizobia and host plants. *Proceedings of the National Academy of Sciences of the USA* 104: 10282-10287.
- Frank, B., 2005. On the nutritional dependence of certain trees on root symbiosis with belowground fungi (an English translation of A.B. Frank's classic paper of 1885). *Mycorrhiza* 15: 267-275.
- Gale, W.J., Cambardella, C.A. and Bailey, T.B., 2000. Root-derived carbon and the formation and stabilization of aggregates. *Soil Science Society of America Journal* 64: 201-207.
- Green, L.E., Porras-Alfaro, A., and Sinsabaugh, R.L., 2008. Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. *Journal of Ecology* 96: 1076-1085.
- Gunningham, N., 2007. Incentives to improve farm management: EMS, supply-chains and civil society. *Journal of Environmental Management* 82: 302-310.
- Khidir, H.H., Eudy, D.M., Porras-Alfaro, A., Herrera, J., Natvig, D. O. and Sinsabaugh, R.L., 2008. A general suite of fungal endophytes dominate the roots of two dominant grasses in a semiarid grassland. *Journal of Arid Environments* 74: 35-42.
- Kiers, E.T., Leakey, R.R.B., Izac, A.M., Heinemanen, J.A., Rosenthal, E., Nathan, D. and Jiggins, J., 2008. Ecology: agriculture at a crossroads. *Science* 320: 320-321.
- Kuldau, G. and Bacon, C., 2008. Clavicipitaceous endophytes: their ability to enhance resistance of grasses to multiple stresses. *Biological Control* 46: 57-71.
- Lairon, D., 2010. Nutritional quality and safety of organic food. A review. *Agronomy for Sustainable Development* 30: 33-41.
- Lee, K., Pan, J.J. and May, G., 2009. Endophytic *Fusarium verticillioides* reduces disease severity caused by *Ustilago maydis* on maize. *FEMS Microbiology Letters* 299: 31-37.
- Lombard, K.A., Forster-Cox, S., Smeal, D. and O'Neill, M.K., 2006. Diabetes on the Navajo nation: what role can gardening and agriculture extension play to reduce it? *Rural and Remote Health* 6: 640.
- Lucero, M.E., Unc, A., Cooke, P., Dowd and Sun, S., 2011. Endophyte microbiome diversity in micropropagated *Atriplex canescens* and *Atriplex torreyi* var *griffithsii*. *Public Library of Science One* 6: e17693.
- Lynch, J.P., 2007. Roots of the second green revolution. *Australian Journal of Botany* 55: 493-412.
- Mann, H., 1848. Education and national welfare. Twelfth annual report of horace mann as secretary of Massachusetts State Board of Education. Massachusetts State Board of Education. Available at: <http://usa.usembassy.de/etexts/democrac/16.htm>.

- Moran, M.S., Peters, D.P.C., McClaran, M.P., Nichols, M.H. and Adams, M.B., 2008. Long-term data collection at USDA experimental sites for studies of ecohydrology. *Ecohydrology* 1: 377-393.
- Müller-Stöver, D., Hauggard-Nielsen, H., Eriksen, J., Ambus, P., and Johansen, A., 2012. Microbial biomass, microbial diversity, soil carbon storage, and stability after incubation of soil from grass-clover pastures of different age. *Biology and Fertility of Soils* 48: 371-383.
- Okon, Y., 1985. *Azospirillum* as a potential inoculant for agriculture. *Trends in Biotechnology* 3: 223-228.
- Ortiz, O., 2006. Evolution of agricultural extension and information dissemination in Peru: an historical perspective focusing on potato-related pest control. *Agriculture and Human Values* 23: 477-489.
- Ortiz, R., Crouch, J.H., Crossa, J., Crouch, J.H., Crossa, J., Braun, H.J., Dodds, J.H., Trethowan, R., Ferrara, G.O. and Iwanaga, M., 2007. High yield potential, shuttle breeding, genetic diversity, and a new international wheat improvement strategy. *Euphytica* 157: 365-384.
- Peters, D.P.C., Pielke, Sr. R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S. and Havstad, K.M., 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences USA* 101: 15130-15135.
- Peters, D.P.C., Sala, O.E. and Allen, C.D., 2007. Cascading events in linked ecological and socioeconomic systems. *Frontiers in Ecology and the Environment* 5: 221-224.
- Peters, S.J., 2006. Every farmer should be awakened: Liberty Hyde Bailey's vision of agricultural extension work. *Agricultural History* 80: 190-219.
- Pinstrup-Anderson, P. and Hazell, P.B.R., 1985. The impact of the green revolution and prospects for the future. *Food Reviews International* 1: 1-25.
- Plett, J.M. and Martin, F., 2011. Blurred boundaries: lifestyle lessons from ectomycorrhizal fungal genomes. *Trends in Genetics* 27: 14-22.
- Richardson, A.E., 2001., Prospects for using soil microorganisms to improve the acquisition of phosphorus by plants. *Functional Plant Biology* 28: 897-906.
- Rodriguez, H. and Fraga R., 1999. Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances* 17: 319-339.
- Rodriguez, R. and Redman, R., 2008. More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. *Journal of Experimental Botany* 59: 1109-1114.
- Sanchez, P.A. and Swaminathan, M.S., 2005. Cutting world hunger in half. *Science* 307: 357-359.
- Schardl, C.L., Leuchtman, A. and Spiering, M.J., 2004. Symbioses of grasses with seedborne fungal endophytes. *Annual Review of Plant Biology* 55: 315-340.
- Stanger, T.F. and Lauer, J.G., 2008. Corn grain yield response to crop rotation and nitrogen over 35 years. *Agronomy Journal* 100: 643-650.
- Swaminathan, M., 1968. Presidential address, agricultural science section the age of algeny, genetic destruction of yield barriers and agricultural transformation, Varanasi, 1968.
- Swaminathan, M.S., 2010. From green to an evergreen revolution, In: *Science and sustainable food security: selected papers of MS Swaminathan*, World Scientific Publishing Company Pte. Ltd., Singapore, pp. 27-40.

UN Millennium Project, 2005. Investing in development: a practical plan to achieve the millennium development goals. Available at: <http://www.unmillenniumproject.org/reports/fullreport/htm>.

UN Millennium Project, Task Force on Science, Technology, and Innovation, 2005. Innovation: applying knowledge in development. New York. Available at: <http://www.unmillenniumproject.org/documents/Science-part1.pdf>.