



Organic Farming, Soil Health, and Food Quality: Considering Possible Links

J.R. Reeve^{*,1}, L.A. Hoagland^{**}, J.J. Villalba[†], P.M. Carr[‡],
A. Atucha[§], C. Cambardella[¶], D.R. Davis^{††}, K. Delate^{‡‡}

^{*}Department of Plants Soils and Climate, Utah State University, Logan, UT, United States of America

^{**}Department of Horticulture and Landscape Architecture, Purdue University, West Lafayette, IN, United States of America

[†]Department of Wildland Resources, Utah State University, Logan, UT, United States of America

[‡]Dickinson Research Extension Center, North Dakota State University, Dickinson, ND, United States of America

[§]Department of Horticulture, University of Wisconsin-Madison, Madison, WI, United States of America

[¶]National Laboratory for Agriculture and the Environment, USDA Agricultural Research Service, Ames, IA, United States of America

^{††}Biochemical Institute, The University of Texas, Austin, TX, United States of America

^{‡‡}Department of Horticulture, Iowa State University, Ames, IA, United States of America

¹Corresponding author: E-mail address: jennifer.reeve@usu.edu

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Abstract

That the health of soils, plants, animals, and people are linked is an ancient idea that still resonates. Growing evidence links farm management, soil health, and plant health but relationships among soil health, food crop nutritional quality, and human health are less understood. Numerous studies compare organic with conventional farming in order to shed light on these links. Organic farming systems utilize carbon-based amendments, diverse crop rotations, and cover crops to build soil fertility. These practices increase biologically available soil organic matter and beneficial soil microbe and invertebrate activities, improve soil physical properties, reduce disease potential, and increase plant health. To date, comparisons of nutrient content between organic and conventional foods have been inconsistent. Recent evidence suggests that organically grown fruits and vegetables contain higher levels of health promoting phytochemicals, possibly linked to greater plant stress, rhizosphere microbial communities, and/or lower available nitrogen. But the overlap in management practices among farming systems make broad generalizations difficult. Moreover, environmental and crop species and/or cultivar interactions may exert stronger effects than management. Here we summarize the known factors influencing soil and plant health and link these with food-crop quality and human health. Though this paper draws primarily from research on organic farming, management practices that enhance soil, plant, and human health remain an important goal for all sustainable food production systems.



1. INTRODUCTION

A possible connection between the health of soils, plants, animals, and people is an idea that traces to ancient times. In ancient Greece, Hippocrates is famously quoted as saying “let food be thy medicine and medicine be thy food,” and this idea still resonates, especially among the growing section of the public interested in the role of natural foods in promoting health. Despite the increasing popularity of the idea, the role of healthy soils in plant and animal health is largely unexplored by the scientific community (Doran et al., 1996). Research has tended to focus on the treatment of deficiency and disease rather than the promotion of health, at least until relatively recently. Doran et al. (1996) suggest three avenues by which soil health could affect plant, animal, and human health. The first is through direct toxic effects such as radioactive or chemical

contamination, either naturally occurring or man-made. Second, specific nutrient deficiencies or excesses can have direct effects on both plant and animal health. Third, there might be a positive effect of soil health on plant and animal health.

Organic proponents were among the first to attempt to prove a link between soil and human health, and this has not been lost on the public. After modest beginnings in the early 20th century, since the 1980s organic agriculture has gained increasing scientific and consumer recognition (Heckman, 2006; Vogt, 2007; Paull, 2011; Carr et al., 2013a). In 2011 organic production was estimated at 37.2 million hectares worldwide, a threefold increase since 1999 when data were first collected (FiBL and IFOAM, 2006, 2013). The global market for certified organic food and drink in 2011 was US \$63 billion (Sahota, 2013). Organic sales have more than quadrupled since 1999, making organic food one of the fastest growing food sectors. The vast majority of this demand is in the United States and Europe with Switzerland having the highest per capita consumption (Sahota, 2013). Yearly growth in sales of organic foods in the United States has consistently hovered in the double digits for 2 decades.

Many studies have attempted to identify the motivations of organic consumers, and several review articles have summarized this work (Yiridoe et al., 2005; Hughner et al., 2007; Dimitri and Dettmann, 2012). The primary reported motivations are health concerns, including nutritional quality, freshness, lack of pesticides, and food safety. Other motivations include better taste, concerns over animal welfare, and environmental degradation. Regional variations in motivations are present: environmental concerns dominate in parts of Europe (Yiridoe et al., 2005; Padilla-Bravo et al., 2013), whereas health benefits are the primary motivation for purchasing organic foods in North America (Yiridoe et al., 2005). Overall, organic consumers tend to be more concerned about potential negative health effects of pesticides and genetically modified organisms than other consumer groups, and may also believe organic produce to be more nutritious (Williams and Hammitt, 2001; Siegrist, 2008; Pino et al., 2012). Occasional consumers of organic food cite health reasons as the primary motivation (Pino et al., 2012). Even nonpurchasers of organic food frequently cite a belief that organic food is healthier (Yiridoe et al., 2005). Price is seen as the main constraining factor by many consumers worldwide (Hughner et al., 2007; Padilla-Bravo et al., 2013).

Despite the widespread consumer belief in the superiority of organic foods, research on the topic continues to be plagued with flaws and

inconsistencies. Several high profile metaanalyses conducted in recent years have questioned the belief that organic foods are healthier (Dangour et al., 2009; Smith-Spangler et al., 2012). Other metaanalyses have shown that there are differences between organic and conventional produce that could translate to improved health outcomes for consumers, including increased antioxidants such as vitamin C and polyphenols, lower levels of cadmium (Cd) and pesticide contamination, reduced incidence of antibiotic-resistant bacteria, and less water content (greater dry matter per unit fresh weight) in organic produce (Baker et al., 2002; Benbrook, 2009; Brandt et al., 2011; Smith-Spangler et al., 2012; Barański et al., 2014). Questions about appropriate methodology, bias, and lack of experimental rigor are commonly cited as underlying factors behind the disagreement in the literature.

It is well known that farm management practices impact soil and plant health as well as produce quality (Karlen et al., 1990; Brandt et al., 2011). For example, variety or cultivar, training and pruning system, pest control, type and timing of fertilizer application, time of harvest, and length and type of storage affect product quality (Brandt et al., 2011). The potential for soil quality or soil health to promote the resistance and resilience of plants to abiotic and biotic stress is a challenging but growing area of research (Doran, 2002; Janvier et al., 2007). This research holds a lot of promise for designing farming systems that are less dependent on external inputs for maintaining productivity and resisting pests and disease (van Bruggen and Semenov, 2000). There is also growing interest in developing plant varieties that are better suited to production under biological and reduced input forms of management, as well as varieties that contain greater concentrations of minerals, vitamins, and beneficial phytochemicals for improved human health (Murphy et al., 2007). This specialized information rarely enters the debate on this topic, which tends to focus on whether organic food is healthier. Efforts to understand and link management effects to quality may lead to farming systems that have beneficial effects on both environmental and human health.

Our goal is to summarize the management factors that influence soil health, review the literature on the links between soil and plant health, and then discuss possible links with produce quality and human health, with a focus on nutrition and plant secondary compounds (PSC). Finally, we make recommendations for future research. We draw heavily on organic farming systems research because the organic farming movement has been central to this debate from the beginning of the 20th century, and the growing literature on organic farming systems comparisons provides unique insights into

the effects of management on soil and plant health. Determining and predicting key management practices associated with enhanced soil, plant, and human health remains an important goal of sustainable agriculture. A clearer understanding of the possible links between soil health, plants, and people is the key to improving the quality and healthfulness of foods grown in all farming systems.



2. ORGANIC FARMING AND MANAGEMENT EFFECTS ON SOIL QUALITY/HEALTH

The concept of soil quality or health has received considerable scientific attention over the years (Parr et al., 1992; Karlen et al., 1997; Arshad and Martin, 2002). Soil quality or health is most often defined as the “capacity of a soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health” (Doran and Parkin, 1994). While this definition is nebulous to some, it allows for flexibility. It is unlikely that the same soil characteristics would be desirable in all environments or management systems. Instead of a fixed benchmark, soil quality is assessed by a suite of physical, chemical, and biological indicators which are interpreted in the context of the environment in which the soil occurs, whether natural or managed. In general, soil quality is inextricably linked to soil carbon (C) and organic matter (OM) dynamics, which in turn directly influence soil physical, chemical, and biological function. Organic matter in soil stabilizes aggregates, helps prevent erosion, increases water-holding capacity, and is a source of slow-release nutrients (Karlen et al., 1990). Soil organic matter (SOM) depletion is linked to the decline of soil quality and is highly susceptible to management strategies (Karlen et al., 1990; Ding et al., 2002).

The links between soil quality, long-term soil productivity, and environmental quality are now widely acknowledged, as is the importance of conserving soil as a resource for future generations. Less clear is whether soil health, per se, has a direct effect on human health through food quality. The terms soil quality and soil health are usually used interchangeably, with soil quality often preferred by scientists and soil health by farmers (Harris and Bezdicke, 1994). Others prefer to reserve the term soil health to refer to the biological components of soil quality, especially disease suppression (van Bruggen and Semenov, 2000). The two terms will be used interchangeably in this article. The older term soil tilth generally refers to the physical

characteristics of the soil and the ease by which the soil can be worked, although the description is very similar to soil quality (Karlen et al., 1990).

One of the first attempts to link soil health with plant and animal health was initiated by Lady Eve Balfour, an early supporter of organic farming in the United Kingdom (Stinner, 2007). Her field-scale experiment was unreplicated however, which severely limited the study's significance. Proponents of organic agriculture were not the only people concerned about soil health. Research by soil scientists and agronomists in the early 20th century focused on management practices that could promote soil tilth and productivity (Karlen et al., 1990). One of the best known attempts to test the effects of the new synthetic fertilizers on crops and soils was at Rothamsted in the United Kingdom. This experiment is ongoing and has shown convincingly that SOM declines when the use of manure is discontinued, and that there is a relationship between SOM and yield that cannot be duplicated with synthetic fertilizers alone (Johnston, 1986).

Since the mid-20th century many long-term farming systems studies have been established, some of which are ongoing, demonstrating that management practices such as extended and diverse crop rotations and use of cover crops and animal manures have profound effects on soil and plant health (Stinner and Blair, 1990; Karlen et al., 1990; Edmeades, 2003; Stinner, 2007; Carr et al., 2013a; Delate et al., 2015). Well-managed organic farms generally have enhanced soil quality compared to neighboring conventional farms (Reganold et al., 1993, 2001; Mäder et al., 2002; Edmeades, 2003; Pimentel et al., 2005; Gomiero et al., 2008). Recent reviews and metaanalyses confirm organic farming systems generally increase soil organic C, a key indicator of soil quality, even under zero net-input conditions (Lynch, 2009; Gomiero et al., 2011; Gattinger et al., 2012; Tuomisto et al., 2012).

Not all research indicates benefits to soil quality following adoption of organic farming systems (Hathaway-Jenkins et al., 2011; Tuomisto et al., 2012). This inconsistency is perhaps unsurprising, given the diversity of farming practices among both organic and conventional growers. Some conventional farms use the same soil building practices as organic farms. Differences between organic and conventional farms form a continuum without always a clear separation. It is generally thought that differences in soil quality are due to the greater reliance of organic farms on longer rotations, organic inputs, and other soil building practices, not due to management differences intrinsic to organic farms per se (Edmeades, 2003; Gomiero et al., 2011). However, potential negative effects of pesticides combined with benefits of diverse OM inputs on the structure and function of soil microbial

communities (biological component of soil quality) remains an ongoing and important area of study (Karlen et al., 1990; Janvier et al., 2007; Liu et al., 2007; Reeve et al., 2010; van Bruggen et al., 2015).

2.1 Nutrient Cycling in Organic Farming

Soil fertility in organic systems is maintained by inclusion of soil-building green manures in crop rotations, additions of organic amendments such as composted or raw animal manure, and biochemical processes that convert nutrients to plant-available forms. Plants can take up organic forms of N, particularly in some environments, and this could be important in farming systems relying on mineralization of OM for their N supply (Reeve et al., 2008, 2009). However, optimal organic N fertility management comes primarily through timely release of inorganic N from OM and its subsequent uptake by plants.

Nutrient transformations in soil are closely linked to turnover of biologically active SOM, provided by either recent inputs or accumulated soil reserves. Successful organic farming depends strongly on managing OM to enhance soil quality and supply nutrients. This involves balancing two ecological processes: mineralization of C and N in SOM for short-term crop uptake, and sequestering C and N in SOM to maintain soil quality, including structure and fertility. The latter has important implications for regional and global C and N budgets and water quality (Drinkwater et al., 1998; Kramer et al., 2006) and soil C storage (Lal and Bruce, 1999; Robertson et al., 2000). However, strategies to optimize biological turnover in organic farming are not well developed scientifically.

Heavy long-term use of manures and composts can increase SOM and soil quality while maintaining, if not increasing, yields relative to conventional systems (Edmeades, 2003; Delate et al., 2015). But overreliance on manures can potentially increase excess nutrient buildup and eventual loss with negative environmental consequences. Such losses are generally reduced on organic farms, at least when calculated on a crop yield per unit area basis (Gomiero et al., 2011; Tuomisto et al., 2012; Cambardella et al., 2015), but N and phosphorus (P) leaching from organic systems can be greater than conventional farms when nutrients accumulate in excess (Aronsson et al., 2007; Dufault et al., 2008; Korsath, 2008; Stenberg et al., 2012). Organic systems that rely heavily on external inputs to boost yields are particularly prone to excess nutrient accumulation (De Wit and Verhoog, 2007; Reeve and Drost, 2012). Kirchmann et al. (2007) argue that

matching N supply with plant demand can be particularly challenging under cold-temperate conditions. More research is needed to increase N use efficiency in organic farming by improved matching of soil supply with plant demand.

2.2 Crop Rotation and Green Manure

Well-managed organic farms employ targeted use of manures and composts primarily to supply P, K, and other macro- and micronutrients to meet crop needs, and rely on legume cover crops and forages to supply N, together with winter catch crops to reduce leaching loss of any residual nutrients. Diverse crop rotations which include soil-building crops such as perennial forages are commonly employed. Long rotations that include forage legumes and green manures improve soil physical properties (Reganold, 1988; Karlen et al., 1990; Lal et al., 1994; Gerhardt, 1997), decrease erosion (Lockeretz et al., 1978; Reganold et al., 1987; Gantzer et al., 1991), decrease N leaching potential (Poudel et al., 2002; Kramer et al., 2006), and increase SOM (Lockeretz et al., 1981; Reganold et al., 1993; Drinkwater et al., 1998; Clark et al., 1998; Liebig and Doran, 1999; Pulleman et al., 2000; Pimentel et al., 2005). Enhanced rotations may decrease the need for external inputs by as much as 85% (Davis et al., 2012).

Green manures can be used as cover crops prior to termination as well as to improve soil fertility (Decker et al., 1994), reduce soil erosion (Langdale et al., 1991), sequester soil C (Sainju et al., 2002), increase soil water infiltration and storage (Munawar et al., 1990), and suppress weeds (Teasdale and Daughtry, 1993). In organic farming systems, cover crops are relied on for both weed suppression and enhancement of soil quality (Clark et al., 1998; Snapp et al., 2005). Effective cover crops for organic systems have included combinations of barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.), wheat (*Triticum* spp.), hairy vetch (*Vicia villosa* Roth), and crimson clover (*Trifolium incarnatum* L.), due to their quick establishment, competitiveness, and ease of mechanical termination (Creamer and Bennett, 1997; Nelson et al., 1991).

2.3 Tillage and Soil Health

The benefits of reducing tillage on surface soil physical and chemical properties (Elliott et al., 1987; Karlen et al., 1990; Ismail et al., 1994; Uri, 2000; Green et al., 2005), along with biological properties (Frey et al., 1999; Kennedy and Schillinger, 2006) have been well documented in conventional

systems using herbicide inputs prohibited in organic production. Tillage affects the depth distribution more than net accumulation of soil organic C in some environments (Baker, 2007; Christopher et al., 2009). Since the behavior of many indicators of soil quality (eg, total N, particulate OM, microbial biomass, etc.) are biochemically and structurally linked to soil organic C, it is likely that tillage impacts on these soil properties will be similar to those observed for soil organic C. Recent research indicates that tillage reductions will have a similar impact in organic systems (Gadermaier et al., 2012). Efforts are underway to optimize soil quality improvements by eliminating tillage completely, but so far “no-till” farming has been successful consistently only in conventional systems where synthetic herbicides are used (Carr et al., 2013b). At present, the decreased use of tillage under organic management must be balanced with the need for tillage as a weed control tool on organic farms.

Changes in tillage can have profound effects on plant nutrient availability. As with the impacts of tillage on other soil quality parameters, organic farmers find themselves in a dilemma as they attempt to build soil nutrient reserves with organic amendments while using tillage to control weeds (Teasdale, 2007). Numerous tillage operations, implemented for weed control and seedbed preparation, stimulate SOM decomposition and can deplete biologically active OM pools that are critical for fertility in these systems. The contrasting impacts of tillage and organic amendment inputs create a dynamic balance of depletion and renewal in these biologically active pools that controls nutrient supply directly, and indirectly, by influencing the soil chemical and physical environment. Recent research comparing 9 years of conventional no-tillage management with organic management indicated that organic farming systems which include cover crops and receive applications of livestock manure can provide greater long-term soil improvement, despite the use of tillage in organic systems (Teasdale et al., 2007).

2.4 Organic Farming Impacts on Soil Biology

Organic farmers have long realized the importance of soil organisms and have pioneered and promoted the use of numerous practices that increase microbial activity and diversity. Management practices employed by organic growers such as the use of composts and manures, cover crops, and diverse crop rotations have been reported to increase biologically available forms of OM (Wander et al., 1994; Marriott and Wander, 2006; Fließbach et al., 2007), and increase the activities of beneficial soil microbes (Elmholt, 1996; Gunapala and Scow, 1998; Fließbach and Mäder, 2000) including

invertebrates (Werner and Dindal, 1990; Neher, 1999). In addition, organic systems have been shown to have more microbial biomass C, greater microbial community diversity, and higher microbial activity than conventional systems for a variety of grain, vegetable, and fruit production systems (Schjønning et al., 2002; Mäder et al., 2002; van Diepeningen et al., 2006; Melaro et al., 2006; Monokrousos et al., 2006; Tu et al., 2006; Widmer et al., 2007; Esperschütz et al., 2007; Reeve et al., 2010; Gomiero et al., 2011). The more highly diverse microbial communities have been shown to transform C from organic residues (Fließbach and Mäder, 2000) into biomass at a lower energy cost (Fließbach et al., 2000), thus resulting in higher microbial biomass within the organic systems. Biological properties of the soil maintain nutrient cycling and soil structural properties. In addition, a growing body of literature supports a connection between biologically diverse and active soils and plant health (see Section 3.3 for more detailed discussion on soil-plant health effects).



3. LINKS BETWEEN SOIL HEALTH AND PLANT HEALTH

Links between aspects of soil and plant health have been well known to growers and scientists alike for generations (Karlen et al., 1990). Soil quality effects on plants generally fall into three categories: physical, chemical, and biological effects. Soil physical properties such as soil structure, porosity and bulk density directly affect rooting depth, water availability and aeration. Soil chemical properties influence nutrient availability as well as issues of salinity and sodicity, all of which affect plant productivity and health. Biological processes affect both physical and chemical properties in soils and also have direct positive and negative effects on plant health. Demonstrating the beneficial effects of soil organisms on plant health has been the most challenging causal link to establish, however, with findings frequently inconsistent. The effects of soil organisms on plant growth and health remains an ongoing and active field of research.

3.1 Soil Physical Properties and Plant Health

Organic matter has a disproportionate effect on soil physical properties which, in turn, affect plant health and yield (Wagner and Wolf, 1999). Organic matter, longer rotations, and use of cover crops decreases bulk density and increases porosity which improves soil conditions for root growth (Reganold, 1988;

Lal et al., 1994; Gerhardt, 1997; Zhang et al., 1997; Seiter and Horwath, 2004). When soil porosity is reduced, compaction increases. Soil compaction increases the amount of pressure the root must exert for growth and decreases soil aeration which also has a direct negative affect on root growth (Marschner, 1995). Reduced root growth limits the volume of soil the plant explores for nutrients and water and may increase the effects of competition from weeds. Kautz et al. (2013) suggest that more work is needed on the role of the deeper soil profile in root growth and plant nutrient acquisition in which soil structure is critical.

Soil structural problems such as reduced soil porosity can inhibit water infiltration and decrease water holding capacity. Reduced soil moisture directly impacts the plant's ability to take up nutrients and withstand drought (Pinamonti, 1998). Lotter et al. (2003) found organically managed crops outperform their conventional counterparts under drought and torrential rain conditions. This is generally attributed to improved water capture and retention under organic management (Werner, 1997; Colla et al., 2000). However, bulk density is not always improved as a result of organic management, despite higher inputs of SOM in organic systems (Colla et al., 2000). This is likely due to increased tillage and equipment passes needed to control weeds on organic farms.

3.2 Soil Chemical Properties and Plant Health

The impact of OM on soil chemical properties has profound effects on plant growth and yield. A direct source of slow-release nutrients, SOM leads to improved chelation of microelements, helps buffer soil pH, and increases soil cation and anion exchange capacity which improves plant nutrient availability and decreases leaching potential (Weil and Magdoff, 2004). Use of composts and manures not only influences the quantity of SOM but contributes reactive humus-like substances that influence nutrient chelation, supply, and storage (Chen et al., 1998; Rivero et al., 2004). Use of manures and composts has been shown to increase the long-term availability of P in calcareous soils by forming coatings on soil particles that inhibit P complexation chemistries (Grossl and Inskeep, 1991; Doner and Grossl, 2002). Reeve et al. (2012) showed a single application of dairy manure compost to dryland calcareous soils retained improvements in soil organic C, available P, and yield of winter wheat 16 years later. Similar findings were reported for repeated light applications of biosolids for similar accumulated total application rates on conventional farms (Cogger et al., 2013).

Improvements in soil nutrient availability lead directly to improved plant health and increased yield potential. Plant yield is an important but potentially complicating factor. There is evidence that plant health (susceptibility to pests and diseases) and nutritional quality are reduced when large quantities of soluble nutrients are supplied with the goal of maximizing yields (see Section 4.2), and it is certainly possible for a plant to be healthy and low yielding. Nevertheless, optimizing yield is an important overall goal of farming and can be an indicator of plant health when considered in conjunction with other variables. When organic fertilizers are supplied in sufficient quantities and weeds and other pests are adequately controlled, yields from organically managed systems can equal or even exceed those of conventional systems (Edmeades, 2003; Delate et al., 2015). This is not surprising, as theoretically there is no reason organic crops should not perform as well as conventional crops when adequate nutrients and pest protection are provided. However, variable soil and climatic conditions make it more challenging to produce crops organically in some places than in others, and total OM inputs and/or number of N-fixing cover crops included in the rotation are often constrained by availability and cost (Dobermann, 2012).

In general, literature reviews and metaanalyses have shown organic yields to be 60–100% that of conventional systems with some regions and crops performing better than others. In a metareview of 316 crops in 66 studies, Seufert et al. (2012) show that average yields are 25% lower in developed countries and that the yield discrepancy drops to 20% when data from developing countries are included. Similar results were found by de Ponti et al. (2012). Earlier studies have found smaller yield differences, although this is likely due to less restrictive criteria when making comparisons (de Ponti et al., 2012; Reganold, 2012). It should be noted that the yield differentials reported in the literature were compared at the plot or field level and the discrepancy could well be higher if large areas were converted to organic production, as competition for organic inputs would be greater (de Ponti et al., 2012). Negative effects of weed competition and asynchrony between N mineralization and peak plant needs are the most cited reasons for yield discrepancies. Breeding crops specifically adapted to weed competition and low input environments is an active area of research that has potential to reduce the yield gap between organic and conventional systems (Murphy et al., 2007).

There are instances when organic farming practices have been shown to outperform conventional fertilizers in terms of plant response. This occurs

primarily on degraded land where soil structural problems rather than fertility limit plant performance, or when very large quantities of organic materials or extended rotations are used (Edmeades, 2003). Increased crop response with organic fertilizers or combinations of organic and soluble fertilizers is often documented in the tropics where problems with soil degradation are most widespread (Place et al., 2003). Including the implications of ongoing land degradation as a result of conventional farming practices in assessments of future yield potential and sustainability remains an ongoing challenge. Further research is needed to quantify yields of organic farming at regional scales as well as include the effects of other ecosystem services such as benefits to soil quality and biodiversity. It remains to be seen whether a fundamental conflict exists between high yields and plant resistance to pests and diseases through secondary compound production (see Section 4.2).

3.3 Soil Biological Effects on Plant Health

Soil organisms play a central role in the breakdown of OM, the mineralization and immobilization of nutrients in soil, and in maintaining soil structure. Hence, soil organisms are crucial to soil function and plant health even though their role tends to be marginalized in current soil fertility recommendations. Soil organisms also directly influence plant health by altering physiological and development processes, facilitating nutrient and water uptake, and helping plants tolerate biotic and abiotic stress (Philippot et al., 2013). These interactions occur largely in the rhizosphere, a narrow zone of soil that surrounds and is influenced by plant roots. Plants signal and support rhizosphere organisms by actively and passively releasing up to 40% of their photosynthetically derived C through root exudates, mucilage, and sloughed off root cells (Bais et al., 2006). The number of microbial cells inhabiting the plant rhizosphere greatly outnumbers plant cells, and the community of organisms present at this interface is often referred to as the second genome of the plant, or its microbiome (Berendsen et al., 2012). The plant microbiome is now widely considered to be crucial for maintaining plant health in natural and managed ecosystems by increasing access to water and nutrients and modulating resistance to pests and disease.

There is a long history of interest and research in plant growth promoting rhizobacteria (PGPR) and plant growth promoting fungi (PGPF). PGPR such as *Azospirillum* have been shown to produce various plant growth promoting substances and fix atmospheric N, thereby increasing plant

productivity (Dobbelaere et al., 2003). Other studies have demonstrated that PGPR and PGPF species stimulate root development (Lee and Song, 2007), help plants withstand drought (Mayak et al., 2004; Hardoim et al., 2008), make plants less attractive to grazing by herbivores above- and belowground (Soler Gamborena et al., 2005; Staley et al., 2007), suppress infection by plant pathogens (Raaijmakers et al., 2009), increase trace element uptake (Rana et al., 2012), and increase antioxidants in fruits and vegetables (Nautiyal et al., 2008; Lingua et al., 2013). Consequently, there has been substantial research to isolate specific PGPR and PGPF for use as inoculants. Improvements in plant health with the application of these inoculants in greenhouse studies with soilless potting mixes are often dramatic. However, while microbial inoculants have improved plant growth in soil with low microbial biomass (Fließbach et al., 2007), results of many field trials are inconsistent (Morrissey et al., 2004; Mark et al., 2006; Cummings, 2009).

Many researchers believe that managing soil organisms *in situ* as opposed to adding inoculants may ultimately prove most successful. For example, one area of research that has received considerable attention is the identification of management practices that induce disease suppressive soil. When a soil is “disease suppressive,” a pathogen fails to infect a plant and cause disease despite the presence of a susceptible crop host and environmental conditions conducive to disease development. Suppressiveness in such soils is thought to result from increased populations of beneficial microbial species that suppress pathogen infection via mechanisms that include competition for resources, production of antimicrobial compounds, parasitism, and induction of enhanced defensive capacity in plants (Janvier et al., 2007). Field studies investigating disease suppressive soil have demonstrated that a wide variety of beneficial microbial taxa are enriched in these soils, and these organisms are thought to work together in a consortium to synergistically suppress plant pathogens and promote plant growth (Kyselkova et al., 2009; Mendes et al., 2011; Watrous et al., 2012).

Organically managed systems have been shown to enhance biological properties and processes, and have greater pathogen suppressive activity (Drinkwater et al., 1995; Mäder et al., 2002; van Diepeningen et al., 2006; Gomiero et al., 2011). For example, Lotter et al. (1999) looked at the incidence of *Phylloxera*-related (*Daktulosphaira vitifoliae*, Fitch) grapevine (*Vitis vinifera* L.) root damage on organic and conventionally managed vineyards in California. They found that while *Phylloxera* damage was the same, root necrosis as a result of the damage was significantly lower in the organically managed vineyards. Necrosis was correlated with *Phylloxera*

populations only in the conventional vineyards and there was an inverse relationship between root necrosis and SOM. Similarly, Liu et al. (2007) found soil collected from certified organic farms and “sustainable farms,” where synthetic fertilizer was applied but pesticides were not used, suppressed *Sclerotium rolfsii* compared with soil collected from conventional farms in greenhouse assays. *S. rolfsii* is the causal pathogen of southern blight, a widespread disease infecting numerous field, horticultural, and ornamental crops. While soil quality was superior from samples collected on the organic farms, the researchers were unable to specify a particular biological, chemical, or physical trait that explained the enhanced disease suppression of the organic soils.

Studies conducted under controlled conditions have demonstrated that composted organic materials can increase the abundance and activity of beneficial microbial antagonists and result in the suppression of a wide variety of soilborne and foliar pathogens (de Brito Alvarez et al., 1995; Hoitink and Boehm, 1999; Stone et al., 2001; Krause et al., 2003; Castano et al., 2011). Organic fertility amendments, including compost, manure and biochar, have increased soil microbial activity and mediated diseases caused by soilborne and foliar pathogens in field trials; however, results have not been as consistent as in controlled studies (Drinkwater et al., 1995; Stone et al., 2003; Rotenberg et al., 2005; Darby et al., 2006; Atucha and Litus, 2015). Biologically based fertility amendments vary widely in their capacity to suppress plant pathogens, and the suppressive activity of individual amendments remains hard to predict (Janvier et al., 2007; Bonanomi et al., 2010). The suppressive activity of compost amendments is known to depend on the feedstocks and methods used during the composting process (Hoitink and Boehm, 1999), but site-specific environmental conditions, including the composition of resident microbial species, could also influence suppressive activity in field environments. Cover crops and green manures can enhance pathogen suppression (Abawi and Widmer, 2000). In some cases, the suppressive activity of green manure crops has been correlated with increased populations of microbial taxa known to play a role in pathogen suppression. For example, Postma et al. (2008) found grass-legume green manures to be correlated with increased populations of *Lysobacter* spp. and suppression of *Rhizoctonia solani*. Similarly, Hoagland et al. (2012) found cultivation of annual and perennial wheat cover crops as green manures to increase populations of antagonistic *Pseudomonas fluorescens* and suppress several soilborne pathogens and nematodes that commonly incite apple replant disease. Additional research identifying practices that consistently induce suppressive

activity, along with the mechanisms regulating suppressive activity, is needed to help organic growers more effectively manage plant pathogens and increase plant health.

The benefits conferred by microbial symbionts which help plants acquire mineral nutrients is another important factor in regulating plant health. Harnessing the power of these symbionts is often seen as crucial for maintaining crop productivity while reducing the harmful environmental effects resulting from over application of fertilizers. One of the most well-studied symbiotic relationships involve rhizobia. Organic farmers have long recognized the value of rhizobial associations with legume plants and regularly include legumes in their crop rotations to help meet N fertility needs (see Section 3.2). The benefits conferred by indigenous versus inoculated rhizobial strains remains unclear, with some studies suggesting that native or naturalized rhizobial species can have greater symbiotic efficiency than inoculants (Ballard and Charman, 2000). Other studies suggest that inoculant strains are superior to resident strains and that resident species compete and negatively impact symbiotic relationships between the inoculant and legume host (Ballard and Charman, 2000). Organically managed fields have been shown to contain a greater diversity of rhizobial isolates than conventionally managed fields, but further understanding of rhizobia ecology and function as related to specific organic management practices is needed to improve N fixation in these agroecosystems (Grossman et al., 2011).

Arbuscular mycorrhizae (AMF) are another microbial symbiont that directly benefits farmers. Arbuscular mycorrhizae are well known for their potential to help plants acquire nutrients, most notably P. Hodge et al. (2001) demonstrated that AMF can also accelerate decomposition of organic materials and directly transfer nutrients from these materials to crop plants. This trait is particularly valuable in organic farming systems where growers rely on decomposition of organic materials to supply nutrients. Arbuscular mycorrhizae can help plants tolerate drought and provide protection from various soilborne pathogens (Wehner et al., 2010). They can also increase plant production of secondary compounds (Toussaint et al., 2007; Lingua et al., 2013). In a study conducted by Song et al. (2010), it was shown that AMF can form connecting networks between plants that convey resistance-inducing signals to neighboring plants, resulting in the suppression of *Alternaria solani*, a foliar pathogen that causes early blight in tomatoes (*Solanum lycopersicum* L.). Over 80% of terrestrial land plants, including most agronomically important crop species, form associations with AMF. Individual AMF species vary in the functional benefits provided to their crop hosts. Furthermore, the

abundance and diversity of AMF assemblages are impacted by agricultural practices such as tillage, fertilization, and crop diversity (Verbruggen and Kiers, 2010).

Organic management has been shown to increase the colonization potential as well as species composition and richness of AMF on a number of different crop plants (Douds et al., 1993; Ryan et al., 1994; Dann et al., 1996; Werner, 1997; Gosling et al., 2006, 2010; Verbruggen et al., 2010). Some studies have suggested that organic farming may select for species that are more adapted/effective at enhancing nutrient uptake compared to systems that utilize large amounts of highly soluble fertilizers and biocides (Gosling et al., 2006). A recent study found that AMF isolated from conventional and organically managed soils reduced P leaching, but AMF isolated from organically managed soils had a greater negative effect on subsequent plant growth compared to AMF isolated from conventional soils (Verbruggen et al., 2012). A drawback of many studies on AMF is that they are conducted in the greenhouse using isolated inoculum. Like most symbionts, supporting AMF represents a cost to the plant in terms of C allocation and there is likely to be a tradeoff for maintaining these relationships in field settings. Also, mycorrhizal species are not consistently beneficial to crop hosts, with some even acting as parasites (Kogel et al., 2006). Research on the effects of AMF in the field has been much more limited and the outcomes often more difficult to predict than greenhouse studies (Gosling et al., 2006; Ryan and Kirkegaard, 2012). Clearly, more research identifying specific management practices that shape the composition of AMF community assemblages is needed to help organic growers realize the full benefits provided by these symbionts.

Understanding how to selectively enhance soil organisms that work synergistically with crop plants has potential to increase plant health and productivity, reduce agriculture's reliance on external inputs, and improve food-crop nutrition. Soil type and management are arguably the most important factors shaping soil and rhizosphere communities, but plants are also able to recruit individual microbial taxa and selectively shape the composition of the rhizosphere (Berg and Small, 2009). Different plant species host divergent rhizosphere community assemblages and these differences can drive corresponding changes in the composition of bulk soil (Bergsmann et al., 2005; Berg and Small, 2009; Ladygina and Hedlund, 2010). A number of studies have provided evidence that plant genotype can also influence rhizosphere community structure (Germida et al., 1998; Micallef et al., 2009; Lundberg et al., 2011; Pfeifer et al., 2013). These studies suggest

plant breeders could select for beneficial plant–microbial interactions. In a classic study that supports this hypothesis, [Smith et al. \(1999\)](#) identified three quantitative trait loci in tomato associated with suppression of the pathogen *Pythium torulosum* by *Bacillus cereus*, a beneficial soil organism that enhances plant growth.

Recent studies have provided evidence that varieties bred for the conventional high-input sector lack important traits needed to optimize plant health under organic and low-input conditions ([Lammerts van Bueren et al., 2002](#); [Wolfe et al., 2008](#)). Some researchers have suggested that breeding programs conducted under high-input conditions may have inadvertently selected against beneficial root–microbial relationships because of the high metabolic costs associated with supporting these organisms. Consequently, varieties selected in these systems would struggle when planted in low-input environments where plants rely on microbial interactions to maintain plant health. For example, [Kiers et al. \(2007\)](#) found that compared to older soybean (*Glycine max* L.) varieties, modern varieties selected in high soil-N environments have less capacity to discriminate between effective and ineffective rhizobial strains, resulting in reduced fitness when plants must rely on these mutualists to obtain N. Identifying the genetic and environmental factors that regulate C partitioning to plant roots will help plant breeders obtain the knowledge needed to begin to select for beneficial plant–microbial interactions.

Identifying agricultural practices and selecting new crop genotypes that enhance populations of beneficial soil organisms will require sensitive indicators to quantify functional changes in these communities. Information on the factors regulating soil biological communities has increased dramatically in recent years as a result of next-generation sequencing and other “omics” technologies. These tools have demonstrated that soil biological communities are much more complex than previously thought. Knowledge of the functional activities of soil organisms remains limited since most have not been successfully cultured in the laboratory. Soil nematode population structure and function have been shown to be sensitive indicators of N mineralization potential and soil health, and changes in these communities have been used as indicators to help researchers identify the impacts of management practices ([Ferris et al., 2004](#); [Sánchez-Moreno, 2007](#)). For example, [Ferris et al. \(2012\)](#) found nematode populations responded primarily to cover crop management as opposed to compost additions and the relationship between the enrichment footprint of nematode assemblages and the yield of organically produced lettuce (*Lactuca sativa* L.) were linked. In

contrast, [García-Álvarez et al. \(2004\)](#) found no response of organic management on nematode trophic structure in a broccoli (*Brassicaoleracea* var. *italica*). Coupling “omics” technologies with strategies that overcome culture bias and link changes in soil microbial communities with the larger soil food web has potential to help organic growers further realize the benefits of this integral component of agroecosystems.



4. POTENTIAL MECHANISMS LINKING SOIL HEALTH, PLANT HEALTH, AND FOOD-CROP QUALITY

A large number of environmental conditions, genotype effects, and cultural practices are known to affect plant health and quality. Similarly, a growing number of studies have attempted to show that organic management increases food-crop nutrient concentration. Potential differences could occur through mechanisms such as increased available trace elements from OM additions, increased uptake due to improved cation/anion balance, or increased availability of nutrients through enhanced biological activity or mutualistic plant–microbial relationships. Interactions between management and plant physiology have also gathered increased scientific attention with the growing interest in PSC. In the following section we discuss potential mechanisms for improved food-crop nutritional quality through soil and plant health, evaluate the current evidence, and discuss research needs.

4.1 Nutrient Rich or Biologically Active Soils Lead to Nutrient-Dense Food

A popular idea with organic growers and the public is that soils managed with compost and cover crops are more biologically active and/or richer in available nutrients (with the exception of N, P, and K in low-input extensive systems) than conventionally managed soils and, consequently, food-crops grown on such soils are correspondingly more nutrient dense. Soil characteristics such as parent material, texture, pH, and SOM are certainly associated with nutrient deficiency in humans ([Frossard et al., 2000](#); [Alloway, 2009](#); [Watson et al., 2012](#)). Location (as a proxy for soil forming factors) has been shown to be the strongest predictor of nutrient content (μg nutrient/g plant material) in food crops and forages ([Spiegel et al., 2009](#); [Watson et al., 2012](#)). In addition, soil microbial activity and rhizosphere organisms are known to play an active role in improving nutrient availability and plant tolerance of heavy metals ([Marschner, 1995](#); [Lehmann et al., 2014](#); see also

Section 3.3), and management practices such as additions of green manure, compost, biosolids, and biochar can increase plant uptake of soil-bound Zn and other nutrients as well as enhance the availability of Zn fertilizer (Watson et al., 2012; Gartler et al., 2013; Aghili et al., 2014). These amendments also reduce the uptake of heavy metals like Cd in rice (Liu et al., 2009). Studies documenting increased plant tissue nutrient content in response to rhizosphere organisms are rare, though mycorrhizal infection has been correlated with greater nutrient and secondary compound content in tomato (Cavagnaro et al., 2006; Giovannetti et al., 2012). Studies investigating beneficial microbial inoculants documented greater Fe, Cu, Zn, and Mn in wheat in response to a bacterial isolate (Rana et al., 2012), and greater Cu and Fe in lettuce in response to mycorrhiza (Baslam et al., 2011; Marschner, 1995).

The situation is complicated by plant species/cultivar, tissue type/age effects (Marschner, 1995; Gartler et al., 2013; Lehmann et al., 2014). Tissue age affects plant nutrient content, and species-specific and age-related differences in nitrate reductase activity determine levels of tissue nitrate (Marschner, 1995). There are also species and cultivar-specific differences in selective uptake and nutrient transport mechanisms. Several plants, including lettuce and spinach, readily hyperaccumulate nutrients supplied in the root zone and transport them to the leaves (Marschner, 1995; Gartler et al., 2013). This occurs even at toxic concentrations and is known as luxury consumption. The hyperaccumulation of Cd by rice is particularly problematic worldwide as high intake of Cd by humans affects the renal cortex, causing Itai-Itai disease (Chaney et al., 2005). Other plant species concentrate excess nutrients in roots or vacuoles, while translocation to aboveground portions or fruiting bodies is limited (Marschner, 1995). Some plants are better able to selectively regulate nutrient uptake in the roots (Marschner, 1995).

Further complicating the situation is the interaction of plant growth rate with environmental factors such as soil moisture, temperature, and light intensity. There is generally a positive relationship between soil nutrient availability, plant growth, and tissue mineral content (Marschner, 1995; White et al., 2009; Zou et al., 2012; Miller and Welch, 2013). However, management that rapidly increases growth such as high rates of fertilization and irrigation can cause declines of at least some nutrients due to the “dilution effect” (Jarrell and Beverly, 1981). This occurs primarily in the deficiency range when selective fertilization of one limiting nutrient results in rapid growth and the appearance of other masked nutrient deficiencies (Marschner, 1995). In addition, different nutrients interact at the level of cell

uptake or are affected by differences in phloem transport. Nutrients with low phloem mobility such as Ca are particularly prone to dilution effects, while trace elements generally have moderate phloem mobility compared to N, P, and K. High rates of N fertilizer has been shown to limit Ca uptake and reduce apple quality (Marcelle, 1995). Likewise, overreliance on ammonium-based fertilizers has been shown to limit cation nutrient uptake in acid soils and decrease carbohydrate content in root vegetables through enhanced root respiration (Marschner, 1995).

Nutrient dilutions and interactions could theoretically be more likely to occur in plants fertilized with high rates of selective mineral fertilizers. This has led some to suggest that a more balanced fertilization approach, where the slow release of nutrients through organic residues occurs along with improved plant access to soil-bound nutrients through enhanced microbial activity, can be used to increase plant nutrient uptake and limit deficiencies. It is important to recognize though, that providing a balanced soil nutrient supply can be challenging to manage in both organic and conventional systems. High applications of OM can lead to excessive buildup of P, K, and Na that interfere with uptake or utilization of other nutrients. For example, Ca can be replaced on binding sites by heavy metals, Al, Na, and protons; excess soil P increases plant phytate content and can promote Zn deficiencies; and luxury consumption of K interferes with uptake of Ca and Mg (Marschner, 1995; Alloway, 2009; Lehmann et al., 2014).

It has also been suggested that the effects of cultivar and plant selection on food-crop nutrition may be stronger than that of soil management (Doran et al., 1996; Murphy et al., 2008; Johansson et al., 2014). Recent side-by-side comparisons of old and modern cultivars of grains and vegetables have revealed decreased nutrient contents in modern, higher-yielding cultivars in wheat (Monasterio and Graham, 2000; Garvin et al., 2006; Murphy et al., 2008), maize (*Zea mays* L.) (Scott et al., 2006), rice (*Oryza sativa* L.) (Anandan et al., 2011), broccoli (*B. oleracea* L.) (Farnham et al., 2000, 2011; Davis, 2013), cabbage (*B. oleracea* L.) (Singh et al., 2013), and lettuce (Mou, 2005), but not in potato (*Solanum tuberosum* L.) (White et al., 2009). The declines have been quantified as either (1) negative slopes in plots of nutrient content versus yield, versus cultivar introduction date, or (in broccoli and cabbage) versus head weight, or (2) negative correlation coefficients between the same measures. The declines resemble those caused by the dilution effect from fertilization and irrigation (Jarrell and Beverly, 1981), except that the yield increases derive from selective breeding and hybridization (Davis, 2011) and not from environmental factors. Thus, they may be

termed “genetic dilution effects” (Davis, 2005, 2009) as opposed to previously recognized “environmental dilution effects.”

Further selective breeding is often proposed to ameliorate mineral declines (genetic biofortification) alone or in combination with trace element fertilization (agronomic biofortification) (Garvin et al., 2006; Murphy et al., 2008; Anandan et al., 2011). These approaches have been adopted for relieving nutrient deficiencies in the Global South (Miller and Welch, 2013). But selective fertilization can lead to declines in tissue content of other nutrients (Marschner, 1995). And genetic and environmental dilution effects generally decrease most or all minerals simultaneously, such as 8 of 8 minerals in wheat (Fan et al., 2008) and 9 of 11 minerals in broccoli (Farnham et al., 2011), while breeding efforts may affect single nutrients only. Whether or not biological forms of agronomic biofortification (microorganisms, composts, and cover crops) are more effective at ameliorating dilution effects than biofortification with mineral fertilizers can be answered by testing in randomized experiments containing management and cultivar as factors over a range of input levels. While enhancing microbial activity through the addition of cover crops increases plant uptake of Zn from both soil and fertilizer sources (Aghili et al., 2014), research on this topic is sparse. We know of no studies to date that specifically test the interactions between fertilizer type, cultivar, growth rate, and yield.

The most important test of whether farm management makes a difference in consumer nutrition is through system comparison studies on food-crop nutrient content. A growing number of studies have attempted to show that food grown organically contains greater nutrient contents than conventionally grown foods (Carr et al., 2013a). Studies vary in methodology, with some sampling produce in the market place, others testing produce grown on paired organic and conventionally managed farms, and other comparisons conducted in randomized controlled experiments. The downside of these studies from the mechanistic perspective is that they do not control for potential variations in plant growth rate and yield. However, they do measure potential system wide differences that are relevant to the perspective of the consumer purchasing organic products in the marketplace. We have identified 14 refereed review papers and metaanalyses published in the past 17 years that have attempted to summarize the research comparing organic and conventional food. Seven of these reviews documented at least some support for the idea that organically grown foods have greater nutritional content, including greater concentrations of minerals and vitamins (Woese et al., 1997; Worthington, 2001; Rembalkowska, 2007; Lairon, 2010;

Hunter et al., 2011; Palupi et al., 2012; Barański et al., 2014). However, they acknowledge that differences between organic and conventional food are generally minor and results across studies are sometimes contradictory. Barański et al. (2014) found greater Cd contents in conventionally grown food crops was one of the most consistent reported differences, a finding with potential health concerns. Elevated Cd is associated with contamination of mineral-based fertilizers such as KCl. Palupi et al. (2012) limit their attention to animal products for which more consistent differences are seen for animals produced on grass (required for organic certification). Further five review articles concluded that the evidence was insufficient to draw firm conclusions (Brandt and Mølgaard, 2001; Bourn and Prescott, 2002; Magkos et al., 2006; Winter and Davis, 2006; Johansson et al., 2014). Two additional metaanalyses concluded there was no significant difference in nutritional content between organic and conventional produce (Dangour et al., 2009; Smith-Spangler et al., 2012).

Barański et al. (2014) recently published the most comprehensive meta-analysis to date and at least partly explain these discrepancies. For example, Dangour et al. (2009) limited their dataset to studies using certified organic crops only. This excluded many high quality comparisons conducted on university research farms which were managed organically but not formally certified (Barański et al., 2014). Another potential reason for a lack of difference in the field is that many conventional growers are becoming increasingly conscientious about soil and tissue testing and applying fertilizers, including trace elements, based on need. Concurrently, many organic growers of specialty crops in particular, increasingly fertilize to achieve high yields, hence risking nutrient imbalances through excess OM applications and potentially sacrificing nutrient concentration advantages from slower growing and/or lower yielding plants. The costs versus benefits of different methods for alleviating nutrient deficiencies and improving nutrition is context dependent and difficult to quantify, and efforts to diversify diets may ultimately be the most effective approach (Miller and Welch, 2013).

4.2 Influence of Genetics, Environment, and Management on Plant Secondary Compounds

A second mechanism linking food-crop quality and human health is through PSC. Many plant tissues contain PSC, long recognized as defensive chemicals that deter herbivory via their toxic effects (Cheeke, 1998; Palo and Robbins, 1991). PSC protect plants from damage by insects, birds, fish,

and mammals by limiting how much of any one plant, animals can eat (Coley et al., 1985; Hay and Fenical, 1996; Palo and Robbins, 1991). The term “secondary compound” was coined by scientists who originally believed these chemicals were waste products of the primary metabolism of plants. However, we now realize that the term is misleading as—in addition to the benefits of preventing/reducing plant tissue loss to consumers—PSC are essential for plants with functions as diverse as attracting pollinators and seed dispersers; helping plants recover from injury; protecting plants from ultra-violet radiation; and defending plants against pests, diseases, and pathogens (Rosenthal and Janzen, 1979, Palo and Robbins, 1991; Rosenthal and Berenbaum, 1992).

Genetics, environmental conditions, and farm management have all been shown to influence secondary compounds in fruits and vegetables. Several studies have documented significant differences in bioactive compound contents among cultivars, including antioxidant compounds in cherry (*Prunus avium* L.) (Usenik et al., 2008), blueberry (*Vaccinium* section *cyanococcus* spp.) (Kalt et al., 2001), strawberry (*Fragaria ananassa* Duchesne) (Nelson et al., 1972), and citrus (*Citrus* L.) fruit (Nagy, 1980), unsaturated fatty acids in walnut (*Juglans regia* L.) (Pereira et al., 2008), avocado (*Persea americana* Mill.) (Yanty et al., 2011), olive (*Olea europaea* L.) (Silva et al., 2012), lycopene in apricot (*Prunus armeniaca* L.) (Gündogdu et al., 2013), and resveratrol in grapes (Vincenzi et al., 2013). Environmental factors such as temperature and light also affect the chemical composition of fruit tissue during development. High temperatures (25/30°C) enhance antioxidant activity in strawberry, as well as anthocyanin and total phenolic content, compared with cool day and night temperatures (18/12°C) (Wang and Zheng, 2001). Higher anthocyanin levels in grapes and apple (*Malus domestica* Borkh) skin are usually attributed to the combination of cool overnight temperatures and high levels of sunshine hours during ripening (Reay, 1999; Mori et al., 2005). Insufficient light reduces fruit quality traits like soluble sugar content (Brooks and Fisher, 1926), and secondary metabolite concentrations such as vitamin C and anthocyanin (Harris, 1975; Grisebach, 1982). Variation in elevation between growing regions has been shown to have a marked influence on antioxidant content in cherries, with high elevation orchards producing cherries with higher concentration of antioxidant compounds than lower elevation orchards (Faniadis et al., 2010). Management practices such as cultural system and fertilization have also been shown to influence secondary compounds in plants (Wang et al., 2002, 2008; Brandt et al., 2011). In addition, it has been

suggested that organic agriculture could result in foods with greater concentrations of PSC, mainly for two reasons: (1) plant stress and (2) resource availability.

The absence of synthetic pesticides in organic farming could result in higher exposure of the plant to a variety of biotic stresses prompted by parasitic, bacterial, and fungal diseases or infestation by grazing insects. These stresses stimulate production of natural defense substances such as phenolic compounds (Winter and Davis, 2006; Woese et al., 1997). Some plants deploy their chemical defenses inducibly after defoliation and thus the production (and concentration) of PSC increases dramatically after herbivory (Baldwin, 1998). In addition, herbivore-induced volatiles may “prime” some plants to respond more quickly with the production of greater concentrations of PSC in response to herbivore attack (Engelberth et al., 2004). Soil growth promoting rhizobacteria are often closely related to common soil pathogens and their presence induces production of the defense compounds in plants that are then more fully protected in the event of a pathogen attack (see Section 3.3). Finally, some PSC such as cyanogenic glycosides and glucosinolates occur in the plant as inactive precursors and are activated in response to tissue damage or pathogen attack (Osbourn, 1996). Collectively, these and other factors that put crop plants under stress—many of which are more likely present in organic systems—will likely result in increased concentrations of PSC in plant tissues.

Conventional farming practices typically increase the availability of selected growth resources. Cultivation, irrigation, and fertilization with N, P, and K enhance crop growth and yields, but conventional farming practices can also deplete SOM and may dilute beneficial primary and secondary compounds in plants (Killham, 1994; Wang et al., 2008). In a 10-year comparison of organic and conventional farming practices, flavonoids were greater in organically than in conventionally grown tomatoes (79% increase in concentration for quercetin and 97% for kaempferol) (Mitchell et al., 2007). Such an increase was attributed to lower availability of soil nutrients in organic than in conventional farming practices. Likewise, high N availability in apple trees increased carbohydrate allocation to primary metabolism, which led to rapid growth but reduced production of phenolic compounds and increased the susceptibility of trees to fungal infection (Rühmann et al., 2002).

According to the carbon-nutrient (C/N) balance hypothesis, the concentration of phenolic compounds (C-based defenses) increases in nutrient-poor environments and decreases in nutrient-rich environments like

fertilized soils (Bryant et al., 1983). Organic fertilizers release nutrients more slowly (as discussed in Section 3.2) or may be applied at lower rates due to the expense. Organic management and fertilization increased total phenolics in eggplant (*Solanum melongena* L.) (Raigoón et al., 2010), while organic pears (*Pyrus communis* L.) and peaches (*Prunus persica* L.) had more phenolics, ascorbic, and citric acids and α -tocopherol than conventional peaches and pears (Carbonaro et al., 2002). Maize had 30–50% more phenolics in organic than conventional crops (Asami et al., 2003) and apples from organic orchards had greater concentration of phenols (19%) than conventional apples (Weibel et al., 2000). Conversely, other findings reveal mixed and less clear-cut results regarding the phytochemical composition and antioxidant capacity of organic versus conventional food products (see reviews by Dangour et al., 2009; Lima and Vianello, 2011). Reganold et al. (2010) found greater vitamin C and polyphenol content in some but not other cultivars of organic strawberry.

These discrepancies can be explained by singularities in the physiology of specific species or cultivars. Some enzymes involved in the synthesis of phenolic compounds can be stimulated differently in contrasting plant species and cultivars due to genetic variations or to the specific role that polyphenols play in a certain plant. In addition, distribution of polyphenols within a plant can vary depending on different metabolic needs (ie, direct free radical scavenging, polymerization, tissue repair) (Faller and Fialho, 2010). It has also been claimed that there are multiple and unrelated factors influencing the content of PSC in plants which prevent broad generalizations about the impact of different farming practices (Rosa et al., 2007). Finally, and as described in this paper, differences in biotic and abiotic factors and stress levels (ie, nutrient levels and degree of pest pressure) among different organic plant management systems may be another reason for the aforementioned inconsistencies in PSC responses. Ripening stage and plant age at harvest, weather conditions, amount and type of fertilizer used can translate into variations in PSC content. These factors should all be controlled for in a well-designed scientific comparison but will nevertheless affect differences between organic and conventional produce in the marketplace (Huber et al., 2011).

Barański et al. (2014) conducted the most extensive (343 peer-reviewed publications) metaanalysis to date and revealed strikingly greater contents of polyphenols in organic than in nonorganic crops and crop-based foods with differences ranging from 19 (phenolic acids) to 69% (flavanones) (Barański et al., 2014). Authors of this study identified lack of

statistical power and/or inaccurate statistical approach as the main factors which prevented some previous metaanalyses from detecting composition differences between organic and conventionally raised crops, in addition to study inclusion criteria. However, they also acknowledged that some of the sources of variation described in this section, that is, crop types, species, varieties, agronomic factors (rotation, fertilization, tillage, irrigation regimes), and environment require further research to better understand the relative differences in composition between organic and conventional crops.



5. FOOD-CROP QUALITY AND HUMAN HEALTH

Despite growing evidence that organic management does result in greater concentrations of PSC, several current reviews suggest that evidence of nutrition-related health benefits from the consumption of organic foods is limited (Johansson et al., 2014; Lairon and Huber, 2014), or currently lacking (Dangour et al., 2010; Smith-Spangler et al., 2012), that PSC are not nutrients, and that it is still a matter of debate whether these compounds have any positive effect on health (Dangour et al., 2010; Smith-Spangler et al., 2012). In this section we discuss the role of PSC in plant defense and as therapeutic agents in human and animal health.

5.1 Plant Secondary Compounds: Their Contemporary Role as Prophylactic and Therapeutic Agents

Despite their potential benefits, generalizations about the toxic impacts of PSC on consumers have been the dominant perception of these chemicals until recent years (Cheeke and Shull, 1985; Cheeke, 1998; Provenza et al., 1990; Robbins et al., 1991; Palo and Robbins, 1991). However, PSC now are recognized as providing benefits to consumers via detrimental effects on pathogens (Picman, 1986; Hocquemiller et al., 1991; Robles et al., 1995; Huffman et al., 1998; Lozano, 1998; Kayser et al., 2003; Villalba et al., 2014b), but also through direct positive effects on health (Crozier et al., 2006). Antioxidants, synthesized to protect plants from oxygen free-radicals produced in photosynthesis, enhance the health of animals, including humans. For instance, flavonoids (eg, flavonols, flavones, anthocyanidins) and other phenolic compounds (eg, gallic acid, chlorogenic acids, stilbenes) are widely found in fruits and vegetables with

antioxidant effects (Nijveldt et al., 2001; Del Rio et al., 2013). In fact, the modulatory effects of flavonoids on the immune response may derive from their antioxidant actions (Middleton et al., 2000). Phenols, flavonoids, isoflavones, terpenes, and glucosinolates appear to lower the risk of neurodegeneration and cardiovascular disease, have immunomodulatory properties, and a wide spectrum of tumor-blocking activities (Potter, 1997; Craig, 1999; Drewnowski and Gomez-Carneros, 2000; Del Rio et al., 2013). Stilbenes such as resveratrol and pterostilbene, which also occur in a wide variety of plants like grapes and blueberries, have antioxidant, anti-inflammation and anticancer activities (Bhat and Pezzuto, 2002). It has been reported recently that birds challenged by an increased production of reactive oxygen species after long flights (Catoni et al., 2008) or under thermal stress (Beaulieu et al., 2014) preferentially select foods high in flavonoids to attenuate the oxidative damage.

Polyphenols such as resveratrol and quercetin, which are produced by stressed plants, extend the lifespan of animals by mimicking the beneficial effects of caloric restriction (Baur and Sinclair, 2006). It has been hypothesized (ie, the xenohormesis hypothesis) that some enzymatic systems in consumers have evolved to respond to plant stress molecules (like resveratrol) as indicators of an imminent deterioration of the environment (Baur and Sinclair, 2008). Secondary compounds like resveratrol are not antifeedants per se but “plant stress molecules” which, through evolutionary time, likely became a signal for consumers about stressful environmental conditions, allowing them to prepare for this adversity. In addition to the specific effects of resveratrol at mimicking the effect of caloric restriction, PSC typically promote satiety (Provenza, 1996) and they are bitter, acrid, or astringent and therefore aversive to the consumer (Drewnowski and Gomez-Carneros, 2000). Thus it is likely that caloric restriction (and weight loss) is a general consequence of consuming greater amounts of PSC with fruits and vegetables (Brandt et al., 2011). Finally, PSC like polyphenols, due to their selective bactericidal actions, may provide consumers with probiotic effects that indirectly impact their immune system at the local (eg, intestinal) and systemic level (Provenza and Villalba, 2010).

Consumer behaviors that lead to a sustained ingestion of medicinal PSC at low doses involve a health preventive strategy, which has been referred to as feedforward (Vitazkova et al., 2001; Villalba et al., 2014b) or prophylactic self-medication (Villalba et al., 2014a). Ingestion of these compounds at low doses is not triggered by a physiological need—like in the self-selection of a medicine to attenuate an internal negative physiological state—because

disease or discomfort is most likely absent when those chemicals are ingested. For example, diets high in plant sterols, soy protein, and almonds [*Prunus dulcis* (Mill.) D.A. Webb], lower blood cholesterol comparably to statin drugs (Jenkins et al., 2005). Diets of whole grains, dark green and yellow- or orange-fleshed vegetables and fruits, legumes, nuts, and seeds contain antioxidant phenolics, fibers, and numerous other phytochemicals that reduce blood cholesterol in consumers (Bruce et al., 2000), and eating a variety of fruits and vegetables may decrease the risk of lung cancer (Büchner et al., 2010). Diets rich in phytochemicals decrease incidence of a wide range of diseases such as osteoporosis, kidney stones, cataracts, macular degeneration, dementia, and Alzheimer's disease (Campbell and Campbell, 2006).

5.2 Do Greater Concentrations of PSC Enhance the Health Value of Organic Foods?

Given the evidence on the health benefits of PSC and the typical increase in their concentration when plants are grown under organic practices, is it safe to conclude that organic fruits and vegetables are healthier due to their greater content of PSC? Brandt et al. (2011) attempted a “proportional approach” where they assumed that the health impact of ingesting organic products was solely due to a greater content of PSC in the food, and proportional to the intake of fruits and vegetables by consumers. Based on these assumptions, it was predicted that a 12% increase in PSC for organic products consumed in a diet would correspond to an average increase in life expectancy of 17 days for women and 25 days for men, or an equivalent of weight loss of 390 and 570 g, respectively, since it has been predicted that being overweight by 25 kg reduces life expectancy by 3 years (reviewed by Brandt et al., 2011).

Based on the greater concentrations of polyphenols in organic foods reported by Barański et al. (2014), it was estimated that a switch from conventional to organic crop consumption would result in a 20–60% increase in ingestion of these PSC (without a concomitant increase in caloric intake), representing the amount of antioxidants available in one to two of the five portions of fruits and vegetables recommended to be consumed daily in a healthy diet. Barański et al. (2014) concluded that this dietary change would be significant in terms of human nutrition, provided that the health benefits of consuming more fruits, vegetables, and whole grains are confirmed to be linked to their PSC content. It is likely an incremental increase

of PSC in foods is not linearly related to their bioactivity, or more generally to an increase in health benefits for consumers. Further, the bioavailability of some antioxidants can be very limited due to their low solubility and absorption and rapid metabolism (Fraga, 2007). In addition, considering the tremendous diversity of chemical compounds in plants, there is potential for multiple interactions among PSC and between PSC and other chemicals present in foods (Villalba et al., 2014b). For example, resveratrol and phenolic compounds have been shown to have antagonistic effects, making resveratrol much less bioavailable when phenols are present (Pinelo et al., 2004).

Compounded with the effects of availability, many studies exploring the health benefits of PSC in organic foods seem to focus on their antioxidant activity (Dangour et al., 2010). However, even when antioxidant activity may be relevant to human health, it is not in itself a direct health outcome and evidence linking antioxidant concentrations in foods with specific *in vivo* mechanisms of action for potential human health effects is not clear (Dangour et al., 2010). As an example, many *in vitro* bioactivity tests use phenolic compounds present in plant tissues at concentrations of micromoles to millimoles, whereas after ingestion, these phenolic—parent—compounds are metabolized into different molecules and their concentration in plasma rarely exceeds the order of nanomoles (Del Rio et al., 2013). Some phenolic antioxidants due to their metabolism and absorption kinetics, may protect cells at the gastrointestinal tract level, that is, locally, but not outside the gastrointestinal tract (eg, breast, lung tissues) (Del Rio et al., 2013).

Evidence *in vitro* is available regarding the positive effects of a greater content of PSC in organic food/extracts relative to conventional products. For instance, extracts from organically grown strawberries had greater anti-proliferative effects of colon and breast cancer cells than extracts from conventional controls, an effect attributed to a greater content of PSC with antioxidant/anticarcinogenic properties in these fruits (Olsson et al., 2006). A new “generation” of *in vitro* studies are testing human and microbial metabolites of phenolic compounds at physiological concentrations and, in this context, anticarcinogenic, antiinflammatory, and antioxidant effects are being revealed through mechanisms that range from influencing cell proliferation and death to impacting the expression levels of different signaling genes, such as oncogenes and tumor suppressors (Del Rio et al., 2013).

Consistent with *in vitro* studies, *in vivo* studies indicate an enhanced immune response in animals fed organic diets (Huber et al., 2011; Johansson et al., 2014). For instance, rats fed diets produced from organic crops displayed significant differences in physiology, especially immune status, relative

to rats fed diets based on conventionally grown crops (Średnicka-Tober et al., 2013). Most notably, chickens on organic feed showed an enhanced immune reactivity and a stronger reaction to an immune challenge than chickens on conventional feed (Huber et al., 2010). These authors hypothesize that organic foods, likely because they are produced under more stressful conditions (given earlier), increase resilience in consumers, that is, the consumers' capacity to quickly return to homeostasis after being disturbed by an environmental challenge (Huber et al., 2011). This hypothesis needs further testing as well as hypotheses dealing in general with the health benefits of organic products. There is a limited number of human intervention studies available exploring the impacts of antioxidant/phenolic intake on human health, but several problems have been identified, that is, lack of appropriate controls, improper description of the antioxidant/nutritional composition of the diets assayed, and limited information regarding absorption/metabolism of the parent PSC ingested (reviewed by Del Rio et al., 2013). All these shortcomings may add confounding effects, which limit the interpretation of results and thus warrant further research to better understand the actual benefits of an increment in PSC ingestion or the ingestion of PSC in general on human health.

In conclusion, emerging evidence suggests that PSC in plants—particularly phenolics—at appropriate concentrations and consumed regularly with diet have the potential to provide health benefits to consumers. Organic cultivation practices are more likely to induce some type of change in plants (reduced nutrient availability, susceptibility to pests, changes in gene expression), which may enhance concentrations of beneficial PSC in their tissues. However, this generalization is constrained by environment, plant species, cultivars, cultivation practices within organic and between organic and conventional systems, and type of PSC under study. More epidemiological and intervention studies are needed to better link the commonly reported greater concentrations of PSC in organically versus conventionally raised crops with human health.



6. CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

Health concerns are the primary motivations of many consumers when purchasing organic food. Perhaps surprisingly, very little research has been conducted specifically to evaluate the possible links between organic

farming, soil and food-crop quality, and human health. It is well known that soil management influences SOM, physical properties, chemistry, microbial activity, and community composition. Plants respond to improvements in soil health with increased rooting depth, drought tolerance, and disease resistance. Yields may increase with improved soil health, especially under adverse environmental conditions, or when soil is severely degraded. We know that abiotic and biotic stress, including resource limitation, increases PSC production and that SOM and rhizosphere microbial communities also influence PSC. There is currently less evidence to support the idea that organic farming results in nutrient-dense foods in the form of increased contents of macro- and micronutrients. While relationships certainly exist between soil nutrient density, soil rhizosphere organisms, soil microbial activity, and plant nutrient density, research is sparse and the picture is complicated by plant genetic and environmental interactions. Plant secondary compounds likely have a positive effect on animal and human health, but the mechanism(s) which explain these effects are still unclear and research is ongoing.

While broad evidence for links between soil health, plant health, and human health are starting to emerge in the literature, much remains unclear. More research is needed on OM retention in soil and how input quality and quantity under different environmental conditions influences the effects of tillage on the SOM pool. A better understanding of how to optimize biological nutrient turnover in organic systems to balance nutrient availability and C sequestration, crop productivity, and plant health is needed. In addition, the role of soil microbiome, plant genotype, and crop rotation interactions in modulating both nutrient turnover and PSC production is only just starting to be explored. This area of research could prove particularly important for simultaneously improving our understanding of resource use efficiency, environmental stability, and plant as well as human health in a range of sustainable farming systems. More needs to be known about improving the reproducibility of microbiological-plant interactions in order to increase widespread adoption of these practices.

The nutrient dilution effects of increased yield that can result from irrigation and fertilization are well known, and there is growing research on breeding-induced genetic dilution effects. However, few studies have been conducted to determine how nutrient dilution can be best ameliorated through management. Similarly, studies which explore the potential to optimize yields without compromising PSC production and pest and disease resistance are lacking. Research is ongoing to tease apart the potential effects

of PSC on human health. Recent studies on modes of action question whether antioxidant capacity is the key mechanism at stake, with mechanisms such as immunomodulatory effects being explored. More research is needed to investigate the relative differences between cultivar, environment, and management interactions on PSC production and to increase the number of well-designed human intervention studies. This will allow us to better determine whether organic farming or management, per se, can be used to positively impact animal and human health.

More attention needs to be given to experimental design and protocol in research aimed at determining if there is a linkage between organic farming, soil and food quality, and human health. While this has improved in studies exploring this linkage due to the recent highlighting of experimental design and protocol issues in the literature, problems still exist. For example, soil type, climate, aspect, cultural practices, and cultivar selection must be identical or nearly so when making comparisons, and more attention needs to be given to sequential harvest dates to control for management effects on fruit ripening. Fresh weights need to be reported as well as dry weights, since it is important to be able to consider the effects of nutrient dilution on intake due to water content. More attention needs to be given to the effects of growth rate and yield on final plant nutrient concentrations when making comparisons between management. Finally, more research is clearly needed on appropriate statistical methodologies, especially in emerging fields such as metaanalysis.

Nevertheless, from the point of view of the consumer purchasing foods in the marketplace, it may be that the large variations in climate, soil type, cultivar, input intensity, growth rate, and productivity across farms largely swamps out any potential differences in nutrient concentration due to management. Until researchers are able to provide clear information to growers on which management practices and or cultivars provide the greatest gains in terms of nutrition and health, and growers can gain a premium for such practices in the marketplace, this situation is unlikely to change. Regardless, consumers will likely continue to purchase organic foods because of the disallowance of genetically modified organisms and synthetic pesticides in organic production.

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