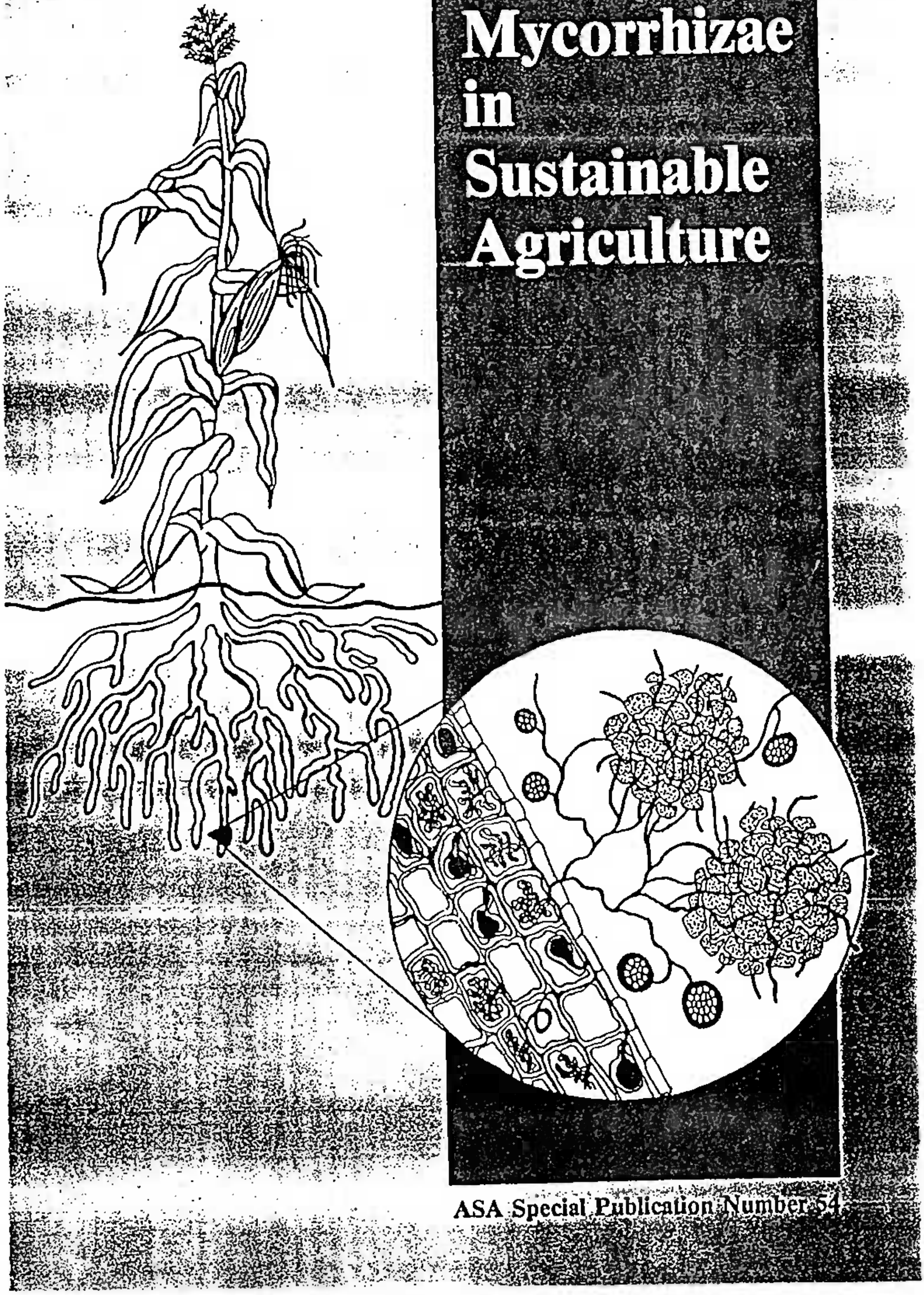
Mycorrhizae in Sustainable Agriculture



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PREFACE[1]

> U.S. agriculture faces an unprecedented problem: How to achieve long-term sustainability in the supply of adequate levels of food and fiber for domestic and international markets, and for humanitarian aid, without degrading the natural environment or resource base, including humans and their communities, upon which agriculture depends. It is the dual nature of this challenge that makes the current situation so daunting. Agricultural scientists must discover and perfect biologically-based systems of farming that are at once productive, profitable, and sustainable for the indefinite future. Most conventional farmers, upon whom adoption of these systems depends, will need a greater measure of confidence in their economic and production characteristics before making the transition to reduced input approaches. (Youngberg, 1990)

The purpose of this special publication is to call attention to a little-known component of this *biologically based farming system*—already discovered but in need of perfection—which has an impact on both production and conservation in sustainable agriculture. Since its inception, the many definitions of sustainability (Gates, 1988) all emphasized the need to protect the production base to ensure reliable access to the product. The production base is a healthy plant-soil system. We recognize now that the unity and interdependence of this system, as well as its health and resilience in the face of natural and cultural stresses, is based to a large but little-known and little-appreciated extent on a myriad of microorganisms that inhabit the interface between plant and soil, the *rhizosphere.*

One type of organism stands out among this host of microbes—*fungi* that penetrate the living cells of plants without harming them, and whose hyphae at the same time range far into the bulk soil, establishing equally intimate contact with the microbiota of soil aggregates and microsites. By doing so, these fungi link plant and soil, transporting mineral nutrients to the plant and C compounds to the soil and its biota (Reid, 1990). They are therefore both agents of plant nutrition and what we will call *soil nutrition*—the vesicular-arbuscular mycorrhizal (VAM) fungi, tools and technology for use in crop production and soil conservation at the same time.

The potential of VAM fungi to enhance crop production is well-recognized, though not well-exploited. The latter is due to a lack of in-depth knowledge of most of the complex symbiotic functions of these plant-fungus associations, and to a lack of practical field experience with them under agricultural, rather than research conditions. On the other hand, the potential, and even the mere involvement of VAM fungi in soil conservation is very little-known (Tisdall, 1991; Miller & Jastrow, 1992). We take the view that the soil is an equal partner in this symbiotic association. Therefore, we speak of the *host soil* as we customarily speak of the *host plant.* This is in line with the critical importance of the soil for sustainable agriculture; soil is not just another instrument of crop production, but a complex, living,

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[1] Contribution of the Horticultural Crops Research Laboratory, Corvallis, OR.

fragile medium that must be protected to ensure its long-term productivity (Reganold et al., 1990).

Why Focus on Mycorrhizae? This agricultural soil that we wish to protect is part of a complex biogeochemical system in which persistent organic structures are formed within a surrounding inert geochemical matrix (O'Neill & Waide, 1981) and whose large-scale behavior is governed by fundamental physiological processes (O'Neill et al.,1991). These processes represent the functioning of many component organisms that contribute to it in concert. How do we decide which component to single out at the experimental level, with reasonable assurance that the work will contribute to the solution of the large-scale problem of sustainability? Why should we choose mycorrhizal fungi to study in the agroecological context over any other organism? And how do we justify and rationalize the need for this or any other small-scale work to funding agencies at the administrative and political levels, whose vision is focused by societal pressures on large-scale imperatives, such as the safety and dependability of essential supplies?

A useful paradigm in this dilemma is the principle of upward constraint by lower-level components on the behavior of higher levels as offered by Hierarchy Theory (Simon, 1962; Webster, 1979). According to this theory, research is justified whenever inhibition of the functions of a lower-level component forms a critical constraint to large-scale system functions (O'Neill et al., 1991). For example, disruption of mycorrhiza-mediated nutrient flux between plant and soil (lower-level component) disturbs soil stability and plant productivity in sustainable agriculture (higher-level system). Thus, the criterion for selection of mycorrhizae from among other components of lesser impact on the large-scale problem is met; VAM fungi form a fundamental link between the biotic and abiotic portions of the system (O'Neill et al., 1991).

Unfortunately, we are apt to be unaware of essential symbiotic relationships while the system is still functioning normally. Thus, for decades, significant progress has been made in ecosystem energy flow and nutrient cycling (two higher-level processes), with the vast majority of ecosystem ecologists unaware of (lower-level) mycorrhizae. We often need to face impending peril, such as the mass extinction of fungi and the destruction of forests that depend on them (Chefras, 1991) before we can focus clearly on a developing upward constraint.

Concepts. The appeal of biologically based systems of farming has fostered efforts in agriculture referred to by many names, such as *alternative agriculture, low-input agriculture*, or *organic farming*. These terms are not synonymous with sustainable agriculture (Thomas, 1990), because each has a special focus of its own. Generally, a change from modern-conventional to post-modern farming systems involves a shift in emphasis on chemicals to natural methods, such as integrated pest management, cover crops, crop rotation, and biological pest control (Comis, 1989; Reganold et al., 1987; Temple, 1990). Such initiatives often focus on concerns of modern agriculture, such as farm economy problems, pollution of surface water and groundwater, pest resistance to biocides, aquifer depletion, soil erosion and salinization, and chemical food contamination.

These concerns have generated discussions regarding sustainable agriculture in relation to use of cover crops, biological control, soil solarization, living mulches, beneficial organisms, as well as pesticide residues and groundwater purity. Research programs in the name of sustainable agriculture have emerged, often to revisit practices of old, such as crop rotation, but more commonly to explore the relationships between sustainable agriculture and integrated pest management, alternative crop nutrient sources and management strategies, soil conservation tillage, and genetic improvement. Most programs underscore the need for interdisciplinary, problem-solving research.

The role of soil microorganisms in sustainable agriculture has been overlooked largely in most conceptual discussions. Those who understand these microbes, however, clearly see their involvement in crop rotation, integrated pest management, fertilizer management strategies, biological control, and soil conservation (Lynch, 1990). Documentation of that involvement has emerged in the literature since about 1965, but the relationship to sustainable agriculture has not been clearly established. For example, the book on alternative agriculture (National Research Council, 1989) published by the National Research Council, refers sparingly to the role played by microbes relative to crop rotation, plant nutrition, N_2 fixation, and pest control. The only references made to VA mycorrhizae were as follows: "Mycorrhizal fungi are important in the uptake of nutrients from soil and in the establishment of vigorous seedling growth in many crop and nursery species," and "Little is known about the genetics of these or other similar organisms or how their association benefits plants. Improvements in their use and establishment of beneficial microorganisms in the rhizosphere could make crop plants more efficient in their use of soil nutrients." Such comments are perfunctory, and only serve to obscure the subject and its importance by sidelining it. Much more could have been said about VA mycorrhizae; there have been thousands of reports on their role in plant and soil biology and in agriculture since 1976.

The contributors of this symposium and publication are dedicated to the objective of painting VA mycorrhizae into the picture of sustainable agriculture. The literature is full of documentation suggesting that their role may be critical if agriculture is to return to the state where luxury levels of farm inputs of fertilizers, pesticides, and other chemicals are decreased to levels that are still economic, yet do not pollute the environment or pose health risks to consumers or handlers.

Microbes in Plant-Soil Biology: An Autocatalytic Cycle. Sustainability of crop production in agroecosystems is dependent on many factors, chief of which is the maintenance of optimum physical structures and chemical, and biological balances in the soil. Major disturbances to such soil systems such as crop removal, cultivation, compaction, chemical applications, hydrologic forces, and extremes in environmental conditions may alter the balances that are necessary for optimum plant growth. Modifications in the soil structure have adverse effects on the chemical and biological processes that support plant growth. Cultivation can set the stage for serious soil loss by erosion. The stratum left behind becomes inadequate for plant productivity as subsoils become the plow layer. In such degraded soil systems, the farmer is obliged to try to add back what has been removed, and that usually is additional fertilizer (Grierson et al., 1991). It is difficult, however, to restore sustainability with regard to the physical and biological components.

In addition to physical alterations, some soils may experience a more gradual loss of soil structure over time due to normal cultural practices. In many agricultural systems, organic matter content will decrease with time, and it is well-known that organic matter and soil colloids are the sites of most of the microbiological processes that occur in soil (Whipps, 1990). Degraded soils loose the balanced organismal composition (Campbell & Greaves, 1990) needed to sustain productivity.

Rhizosphere organisms function in support of plant growth in a variety of ways, and loss in sustained productivity may be due to an impairment of any one of those functions. These functions include chemical reactions by way of the metabolic exchanges of a myriad of microorganisms that are crucial for both plant productivity and soil structure. They must be present, or restored if lost, to make the agricultural plant-soil system sustainable. The VAM fungi play a crucial role in facilitating both microbial and plant functions by acting as mediators of nutrient exchange between them. Thus, we discern a closed chain of cause-and-effect relationships in the role of VAM fungi in the plant-soil system—the fungi improve the health and development of their host by enhancing plant nutrition and disease and stress resistance; the more vigorous plant is a better source of C to the soil, which encourages the activity of the soil biota; the products of microbial metabolism enhance soil aggregation; and better soil structure permits better plant and VAM-fungal growth.

Mycorrhizae in the Plant-Soil System. In all ecosystems, the coupling of plants with rhizosphere microbial processes is optimized by VAM fungi. These fungi form a symbiotic relationship with plant roots, and the fungal symbiont becomes a major interface or connection between the soil and plant. The VAM symbiosis begins with germination of large spores, or other forms of inoculum propagules, such as root fragments, that occur in most soils as a result of their production and release into the soil from previous host roots. Spores germinate and penetrate the root cortical cells, forming specialized haustoria-like structures within the cells called *arbuscules*, where metabolite exchanges take place between fungus and host cytoplasm. Characteristic vesicles usually also form in the cortical cells and function as nutrient storage organs or as propagules in root fragments. The VAM-fungal hyphae also extend from the root out into the soil where they interface with soil particles. Soil (extraradical) hyphae function as absorptive structures for mineral elements and water. Because they can extend out several centimeters from the root, they can effectively bridge over the zone of nutrient depletion around roots and absorb immobile elements from the bulk soil. Soil hyphae also attract other microbes, and together they form water-stable aggregates necessary for good soil tilth. The internal colonization of roots by VAM fungi plus the nutrient and water uptake from soil by the soil hyphae of the fungal symbiont causes pervasive physiological changes in the host plant. Such changes make the VAM plant grow and respond to environmental stresses differently from a non-VAM plant. Not all VAM fungi induce the same kind and extent of change, however. Nevertheless, the hypotheses that VAM plants grow better than non-VAM plants in agricultural soils that may have been degraded by current cultural practices is worthy of validation.

Many of the reactions and interactions of the microflora and fauna that occur in the soil around roots are mediated by VAM fungi that function to deliver mineral nutrients to the host plant in return for a sustained C supply. They also impart other benefits to plants including stimulation of growth-regulating substances and alteration of other chemical constituents in the plant, increased rate of photosynthesis, osmotic adjustment under drought stress, enhancement of N_2 fixation by symbiotic or associative N_2-fixing bacteria, increased resistance to pests and tolerance to environmental stresses, and improved soil aggregation and thus improved soil physical properties and stability. Because of the improved nutritional status of VAM plants, membrane permeability is altered, and this change can greatly alter the quality and quantity of root exudates, resulting in a new microbial equilibrium in the soil surrounding that root, now appropriately called the *mycorrhizosphere*. The chemical and physical effects of the fungal symbiont extending out into the soil creates a whole new dimension, both spatially and biologically. Specific organisms establish special relationships with mycorrhizal fungi that have a net beneficial effect on plant growth. Such discoveries open possibilities for understanding the role of mycorrhizae in N cycling and developing management strategies for improved N economies of agricultural crop plants.

Many studies in the literature report relationships between VAM fungi and specific rhizobacteria such as phosphate solubilizers, biocontrol agents, siderophore producers, hormone producers, etc., but definitive data are largely lacking. The spacial relationships between VAM soil hyphae and these bacteria has not been established, although it is known that the soil aggregates formed around sticky VAM hyphae contain high microbial counts and activity. It was suggested that some of the benefits to plant growth attributed to VAM fungi really belong to the combination with their bacterial associates. This is a hypothesis that needs considerable in-depth investigation.

We believe that VA mycorrhizae can play a major role in the quest for sustained plant productivity in all segments of agriculture. This belief is based on the general hypothesis that agricultural soils have been degraded since the 1800s from their more microbiologically balanced state of the natural ecosystem before cultivation. Soil degradation involved disturbance of the balance by cultivation, monoculture, excessive inputs of pesticides and fertilizers, removal of organic matter from the soil by crop removal and accelerated decomposition without replacement, and erosion. To maintain economic levels of productivity, farmers have been forced to increase inputs. If the goal is to reduce chemical inputs for environmental and health reasons, then mycorrhizal fungi and other beneficial microbes need to be reestablished to a high level of effectiveness to offset the reduced inputs. The literature strongly supports the idea that VAM fungi are the universal compensators needed to accomplish the mission of sustainable agriculture.

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