

Ecological and Genetic Systems Underlying Sustainable Horticulture

Autar K. Mattoo, and John R. Teasdale*

Sustainable Agricultural Systems Laboratory
USDA-ARS, Animal and Natural Resources Institute
Building 001
The Henry A. Wallace Beltsville Agricultural Research Center
Beltsville, MD 20705-2350

*Corresponding author. Fax: 301 504 6491; E-mail address: autar.mattoo@ars.usda.gov

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I. INTRODUCTION

Crop production and food security are high priorities on the list of global concerns to meet the food demands of the growing world population. It has been estimated that over the next 20 or more years agricultural production needs to double from the same area of land (Norman Borlaugh quoted in Smaglik 2006). This poses a higher challenge particularly when a declining trend in crop yields and increasing water shortage is apparent in many nations (Rosegrant and Cline 2003). In the last century, conventional breeding strategies for large-scale farming in concert with fertilizer use and integrated pest management led to higher crop production (Trewavas 2001). Unfortunately, this increase in production was achieved at the cost of impacting the world ecosystems and raising concerns for human and animal health because it relies heavily on chemical inputs of agrochemicals, synthetic fertilizer and heavy machinery driven by fossil fuels (National Research Council 1989). The high usage of non-renewable resources in conventional agriculture also resulted in loss of top soil, reduced soil fertility and contamination of the two major natural resources, water and air (Smil 1997). Preservation of yield and attractiveness, particularly for fruits and vegetables, continues to rely heavily on the use of pesticides.

Thus, agriculture faces unprecedented challenges due to rising energy costs, global climate change, and increasingly scarce production resources. It will become imperative for producers to adopt sustainable systems that rely on natural processes and use inputs as efficiently as possible. Sustainable agricultural systems strive to achieve the

general goals of productivity, profitability, and resource conservation while using local applications of these principles depending on climate, soils, and available markets. There are many approaches to achieving sustainability that can range from organic farming with no synthetic inputs to conventional farming with the latest genetic and technological inputs. In this review we highlight the development of production systems based on sound ecological principles as well as on physiological and genetic principles that hold the most promise for addressing the challenges of the 21st century. In the first section we focus on organic farming because the systems approach that relies on ecological processes is most developed and clearly articulated by practitioners and researchers of this form of agriculture. In the second section, the focus is on genetic systems and how these can underlie and supplement ecological approaches for improving agricultural systems. Finally, in the third section we suggest the importance of integrating ecological and genetic approaches to optimize agroecosystem sustainability.

II. ECOLOGICAL SYSTEMS

A. Conventional versus Organic: Principles and Distinctions

Organic farming is often defined by prohibited substances (e.g. synthetic fertilizers, pesticides, transgenic crops), but organic production can also be defined in positive terms relating to resource cycling, ecological balance and biodiversity. Most organic farmers would agree that their goal is not simply “input substitution,” i.e. substitution of organic forms of fertilizer and pesticide products into production systems that are otherwise unchanged. Instead, the focus

is on designing a new production system that builds the means of fertility and pest management into agroecosystem processes that will support crop production (Drinkwater et al. 1995). Thus, conventional inputs are replaced not just by a different set of approved organic products but by the integrated functions of the agroecosystem itself.

A major principle of organic agriculture is building soil organic matter as the underlying prerequisite for building the capacity to supply essential resources for crop production (nutrients and water) as well as for building the species diversity needed to maintain manageable pest and weed populations. The adage “feed the soil, not the crop” refers to taking a long-term systems approach to building the fertility and resilience of soils rather than taking a short-term approach to supplying growth requirements to crops. It is often difficult to determine the relative efficacy of these approaches to crop production because of the different time scales involved for optimizing each system. Changes in agroecosystem processes associated with converting from conventional to organic management, especially processes based on soil organic matter, can take many years or even decades to reach a new equilibrium,. Thus any assessment of the efficacy of organic production must be conducted over a long-term temporal scale to capture underlying soil dynamics (Drinkwater 2002).

B. Agroecological Principles of Soil Management

Most benefits of organic soil management can be linked with high organic matter inputs to soils. This is accomplished by keeping crops or cover crops continually growing throughout

the year and by adding organic amendments from external sources as needed. Soils with a history of organic farming sequester higher levels of soil carbon than corresponding conventional soils both in horticultural systems (Ciavatta et al. 2008; Melero et al. 2008) and in agronomic systems (Marriott and Wander 2006). Increased soil organic carbon has been associated with increased productivity of soils resulting in higher crop yield potential in organic than conventional systems after soil carbon has become higher in organic systems (Fig. 1). Organic soils with higher organic matter levels often have higher capacity to capture and store essential nutrients, e.g. nitrogen (Marriott and Wander 2006) and water resources (Sangakkara et al. 2008). Higher organic matter also leads to higher soil aggregate stability which is associated with higher microbial and earthworm biomass and mycorrhizal colonization in long-term organic soils (Mäder et al. 2002). High soil organic matter is also associated with richer food webs and higher biological activity that drive soil ecological services (Mäder et al. 2002).

Conservation tillage practices also promote many of the same goals for soil improvement as organic farming systems, including sequestering carbon, improving soil nutrient and water holding capacity, resisting sediment and nutrient losses, and enhancing soil biological activity (Peigne et al. 2007). The adoption of conservation tillage systems in conventional agriculture, particularly no-tillage, has been facilitated by the advent of herbicide technology and transgenic crops for control of weeds, that otherwise would become more problematic with the elimination of tillage. For example,

absence of tillage in organic cropping systems led to lower crop yields due to increased weed competition and lower nitrogen mineralization (Drinkwater et al. 2000). It has been suggested that organic systems can not attain the same degree of soil stewardship because, without herbicides, weed control and seedbed preparation require tillage operations that oxidize soil organic carbon and destroy soil structure (Trewavas 2004). However, research has shown that organic systems, despite the tillage required, can build soil carbon and yield potential of soils beyond that achieved by conventional no-tillage systems (Teasdale et al. 2007). Organic farmers could potentially reduce tillage and gain additional soil benefits by both diversifying rotations to include perennial crops as well as by combining minimum tillage practices with recent technologies for mechanically suppressing high biomass cover crops that can substitute for herbicides in suppressing weeds (these options are discussed below). There also are opportunities for conventional farmers to improve their systems by increasing organic inputs such as by diversifying rotations with cover crops (Calegeri et al. 2008).

C. Soil Fertility and Nutrient Availability

Some have suggested that soil fertility is “fundamentally different” in organic systems than conventional systems (Drinkwater et al. 1995), however, others have concluded that the fundamental processes driving nutrient cycling do not differ but that the primary differences are related to the quantity and quality of inputs (Stockdale et al. 2002). Nutrients delivered in organic forms, either from *in situ* crop or cover

crop residue or from organic amendments, are usually present in lower concentrations than in fertilizers and require large quantities of material either to be grown as a rotational green manure or delivered to fields from off-site locations to meet crop growth requirements. Most organic materials do not contain a large amount of readily soluble nutrients and, hence, nutrient availability in organically farmed soils is dependent on soil processes for nutrient mineralization.

Substrate decay dynamics and nutrient mineralization are affected by soil microbial activity which in turn is affected by soil environmental conditions such as temperature, moisture, and aeration, as well as soil chemical properties, particularly the ratio of carbon and nitrogen (Gaskell et al. 2006). Soil microbes are carbon limited so organic amendments with higher extractable carbon have been shown to increase microbial biomass, microbial respiration, and nutrient mineralization in organic vegetable production systems (Tu et al. 2006; Melero et al. 2008). In general, mature organic farming soils often have lower levels of soluble nutrients, especially inorganic nitrogen, at any given time but have a greater capacity to mineralize nutrients than conventional soils (Drinkwater et al. 1995; Poudel et al. 2002; Miller et al. 2008).

Because soluble nutrients are not readily available and their release depends on microorganism-mediated processes, mineralization is not necessarily synchronized with crop demand (Gaskell et al. 2006, Evanylo et al. 2007). Amendments with a high carbon to nitrogen ratio can immobilize nitrogen into microbial biomass and reduce immediate availability and uptake

by crops (Rodrigues et al. 2006) despite the potential long-term impact high carbon amendments can have on nutrient availability. Most reports of inadequate nutrient availability leading to poor crop yields in organic versus conventional systems have been associated with experiments where organic systems have been maintained for less than 10 years and there probably was insufficient time to develop adequate mineralization potential (Rodrigues et al. 2006; Cavigelli et al. 2008). Most reports of adequate fertility and equivalent yields between organic and conventional systems are based on systems in place for at least 10 years (Pimentel et al. 2005).

In addition to the problem of synchronization, the ratio of nutrients in organic materials may not match requirements of crops. For example, the nitrogen to phosphorus ratio in composted amendments is usually lower than that required by crops, leading to the dilemma as to whether to fertilize according to crop nitrogen requirement and oversupply phosphorus or apply to phosphorus requirements and undersupply nitrogen. Limited manure and compost application to organic fields because of nutrient management regulations limiting phosphorus application to high-P fields led to lower nitrogen availability in many years of a long-term experiment in Maryland (Cavigelli et al. 2008). However, Evanylo et al. (2007) showed that high annual compost rates could meet vegetable crop nitrogen requirements but would not increase phosphorus loss from fields because of improved soil physical properties leading to increased rain infiltration and reduced runoff volume. Thus, although organic farms may arrive at a new equilibrium with higher soil

carbon, microbial activity, and mineralization potential after years of organic inputs, this process will still require careful management to meet the appropriate balance of nutrients required by crops and to avoid the buildup of excess nutrients that can pose an environmental hazard or the depletion of nutrients that could limit yields.

D. Weed, Disease, and Pest Management

Perhaps the most challenging aspect of organic farming is controlling weeds, pests, and diseases without use of agrichemical products that are the mainstay for crop protection in conventional agriculture. Although biologically based alternatives have been explored and some successes have been recorded, their major limitation has been inconsistency compared to the recommended agrichemical standards. For example, in a review of weed suppression by cover crops, Teasdale et al. (2007) found that suppression of weed biomass ranged from 0 to 99% by several cover crop species grown in different areas of the world. Although progress has been made developing biological agents for control of plant diseases, this approach has also been hampered by inconsistent performance (Compant et al. 2005; Roberts et al. 2005). The most promising approach for control of weeds, pests, and diseases is not through identification of single control tactics but through development of integrated systems that maintain populations of unwanted organisms within acceptable bounds (Lewis et al. 1997). This approach seeks to use preventive measures to limit weed/pest populations by a combination of system stresses or “many little hammers” (Lewis et al. 1997; Liebman and

Gallandt 1997). Thus, crop rotation, timing of planting, creating an attractive habitat for natural enemies, tolerant crop cultivars, competitive crop populations, optimizing soil fertility, and avoiding crop stress all may be insufficient alone, but together may limit damage from weeds/pests/diseases to acceptable levels.

Since long-term changes in soil organic matter, nutrient mineralization potential, and biological activity is fundamental to the ecologically based management of organic farming, solutions to controlling weed, pest, and disease populations must also be integrated with these basic soil conditions. Drinkwater et al. (1995) has shown that soil nutrient management can have profound implications for plant-pathogen and plant-herbivore interactions suggesting that the consequences of soil processes in organic systems extend to community level mechanisms for regulating disease and pest populations. In their study of fresh market tomato production on twenty organic and conventional farms, reduced corky root disease was associated with increased microbial activity, particularly cellulolytic actinomycetes, and lack of herbivory was associated with greater abundance and species richness of predators and parasitoids on organic farms.

Additional mechanisms that involve crop responses can also contribute to crop protection. Induced resistance is a series of plant defense responses to invasion by pests or disease organisms that are mediated by the hormones jasmonic acid, salicylic acid, and ethylene (Walters and Heil 2007; Zheng and Dicke 2008). The specific transcriptional and metabolic events associated with induced resistance have

been demonstrated for many crop-pest or crop-pathogen systems. There is generally a metabolic cost to the crop in the form of reduced growth or yield for this induction response and this explains the absence of these processes as a constitutive plant defense mechanism (Walters and Heil 2007). Because these costs are associated with reallocation of limited resources in some instances, the cost to crop growth or the expression of resistance can be a function of resource availability to the crop. For example, nitrogen has been shown to modulate the growth and seed yield costs of *Arabidopsis* to induction of pathogen resistance (Dietrich et al. 2004). These induced responses can also be sensitive to the presence of multiple species of pests and pathogens in an ecosystem that can result in a complex of signaling leading to negative and positive crosstalk between jasmonic acid and salicylic acid pathways (De Vos et al. 2005). Mutualistic symbioses involving mycorrhizal fungi and root nodule forming *Rhizobium* are highly critical to plant nutrient capture in organic systems but also can interact with induced resistance responses to pest or pathogens. These mutualistic organisms have been shown to induce resistance to certain diseases but their function also may be impaired by resistance induction (Walters and Heil 2007). The important legume-rhizobial symbiosis that provides the plant with N and the soil rhizobia with carbon is now thought to be mostly a plant-controlled process (Caetano-Anolles and Gresshoff 1991; Kawaguchi et al. 2002) and this process appears to be interrelated to resistance induction by invading pests or pathogens as well. Thus, the agroecosystem functions of both nutrient acquisition and regulating crop and pest/pathogen

interactions appear to be regulated by important subcellular processes. The linkage of these functions offers exciting management opportunities given greater understanding of these processes in the future.

E. Crop Rotation

A diverse crop rotation is fundamental to addressing the two major obstacles to the successful transition from conventional to organic farming, namely, weed control and nitrogen sufficiency. Most examples of the importance of rotation come from long-term agronomic studies but the principles apply equally to horticultural crops. During the first ten years of the long-term Beltsville Farming Systems Project comparing three organic rotations and two conventional systems, nitrogen availability and weed abundance explained 73% and 23% of the yield difference between conventional and organic maize. However, organic maize grown in a longer, more diverse rotation of maize-soybean-wheat-hay yielded higher, had higher nitrogen availability, and had lower weed abundance than organic maize grown in a standard maize-soybean rotation (Cavigelli et al. 2008). Long-term research in conventional systems showed that first-year maize following alfalfa did not require additional fertilizer nitrogen to optimize yield whereas second- and third-year maize following alfalfa did require fertilizer nitrogen suggesting that alfalfa can substantially meet first-year nitrogen requirements (Stranger and Lauer 2008). Additional research at the Beltsville Farming Systems Project showed that organic rotations with phenologically diverse crops provided a good example of systems-level dampening of soil weed seed

populations (Teasdale et al. 2004) as discussed in the previous section.

Including a perennial sod or hay crop in an organic rotation has many benefits including building soil fertility and reducing weed populations, as outlined above, but it also can contribute substantially to reducing the tillage frequency in the rotation and thus provide many of the same benefits conferred by reducing tillage. Thus, a rotational hay crop may not only provide the nutrients to subsequent crops but also positive long-term changes in soil organic carbon, microbial activity, and aggregate structure (Karlen et al. 2006). It has been argued that increases in organic grain crop yield that result from following a rotational soil-building crop are misrepresented because they do not account for the land and time required to grow the soil-building crop as well (Trewavas 2002). When Olesen et al. (2002) computed the total grain yield across a four-year rotation, the benefit of inclusion of a grass-clover green manure crop in one of four years could not adequately compensate for the yield reduction of leaving one quarter of the rotation out of production of a cash crop. However, Schmutz et al. (2008) showed that fertility from green manure crops incorporated into moderate intensity organic vegetable production systems without livestock or associated manure amendments could be economical.

F. Cover Crops in No-Tillage Systems

Many of the benefits of no-tillage and organic agriculture described above can be magnified by incorporating cover crops into rotations (Sustainable Agriculture Network 2007). Cover crops fix carbon that can input substantial amounts of organic matter to soil without requiring hauling expenses

associated with soil amendments such as manure or compost. Legume cover crops fix nitrogen that can provide a substantial input of nitrogen for succeeding crops (Sainju and Singh 2008). Cover crops capture excess nitrogen and other nutrients from the soil thereby preventing potential losses from the soil system. They cover the soil with a vegetative cover that prevents soil losses during heavy rainfall events. Residue remaining after the cover crop is killed can assist rainfall infiltration and prevent evaporation of soil moisture. They can displace or otherwise interfere with weed and pest populations. For example, organic tomatoes intercropped with turfgrass had higher resistance to leaf blight, higher root colonization by mycorrhizal fungi, higher photosynthetic capacity in the late season, and higher yields than when grown in clean tilled soil (Xu et al. 2008).

Conversely, cover crops can have negative influences on cropping systems if not managed properly (Sustainable Agriculture Network 2007). They withdraw soil moisture reserves that may be essential to production of subsequent crops. They can tie up otherwise available nutrient resources if the carbon-to-nitrogen ratio is too high. They can interfere with planting operations if excessive levels of biomass remain on or near the surface of fields. And they can enhance certain weed and pest populations by providing resources and environmental conditions suitable for those species.

A system for no-tillage planting of tomato transplants into a hairy vetch cover crop was developed by Abdul-Baki and Teasdale (2007) that has been extensively studied at the USDA-ARS Beltsville Agricultural Research Center. This system involves planting a hairy

vetch cover crop on beds in fall, mowing the abundant biomass of vetch after danger of frost in spring has passed, and transplanting tomatoes or other summer vegetable crops through the mulch with a no-tillage transplanter. The system is not organic in that it utilizes fertilizer, herbicides, and fungicides but levels of these are reduced compared to conventional systems. For example, tomatoes grown in the hairy vetch system required approximately half the amount of nitrogen required by those grown in the conventional system to obtain maximum yields (Abdul-Baki et al. 1997). Research over a ten-year period showed higher tomato yields and net returns using the hairy vetch system compared to a conventional black polyethylene system (Abdul-Baki and Teasdale, 2007). Tomatoes in black polyethylene mulch initially grew at a faster rate than those in hairy vetch mulch, presumably because of faster soil warming under the black polyethylene. Later in the season, tomatoes produced greater leaf area and maintained that leaf area over a longer period in the hairy vetch mulch than in the black polyethylene mulch (Fig. 2). Leaf area duration was correlated to yield and could explain the higher yield of tomatoes in the hairy vetch mulch. Higher leaf area was associated with delayed leaf senescence and reduced foliar disease in the hairy vetch grown tomatoes. A molecular basis for delayed leaf senescence and tolerance to diseases in tomato plants cultivated in the hairy vetch mulch has been demonstrated. In hairy vetch-cultivated plants, expression of specific and select classes of genes is up-regulated compared to those grown on black polyethylene mulch (Kumar et al. 2008; discussed below). The expression of the genes associated with

efficient utilization and mobilization of N, higher photosynthetic rates, higher carbon mobilization, sustained reducing power, and defense promotion were at a higher steady-state level in vetch-grown tomato leaves than in plants grown under black polyethylene. The net result was that tomato plants lived longer, delayed leaf senescence, and were more tolerant to diseases. This system will be discussed in depth below as a model system for understanding and designing sustainable horticultural systems in the future.

III. GENETIC SYSTEMS

The discussion in the previous section suggests that agroecosystems function according to carefully regulated processes at several scales from the population level to the molecular level. There is a complex system of metabolic cycles and interacting genetic regulation that underlies soil microbial functions, nutrient cycling, crop production, and other processes that determine agroecosystem performance. It may be presumed that at each level there are key factors that control cycling, outputs and communications among system levels and that may ultimately influence overall system functioning. Agricultural breakthroughs will most likely result from improved understanding and application of these key regulating and signaling factors.

A. Legume Metabolism and Functional Molecules

Among the cover crops, legumes are critical for sustainable agriculture systems because of their ability to fix nitrogen in association with nitrogen fixing bacteria such as *Rhizobium*, providing renewable source of nitrogen and consequently lowering the input of

synthetic fertilizer in agriculture. This will become particularly important as fertilizer nitrogen that is dependent on natural gas for production and petroleum products for transportation becomes increasingly expensive. The focus of this review is on functional and/or signaling molecules that legume cover crops accumulate during growth and development that can profoundly influence the growth and defense potential of succeeding crops. The nutrients and bioactive molecules released during decomposition of cover crop residue and their interactions with crop plant roots within the rhizosphere will define the potential benefits to crop production, produce quality and ecosystem function.

Marketable fruit yields were found to correlate with the carbon (C):nitrogen (N) ratio of the cover crop used, the higher the C:N ratio the lower the yield (Teasdale and Abdul-Baki 1998). Nitrogen release from cover crops is considered a major component that not only replaces the input of chemical fertilizer for robust growth of horticultural crops but also signals beneficial attributes in the subsequent crop (Abdul-Baki et al. 1997). Thus, N-responsive genes, such as *NiR*, *GSI*, *rbcL*, *rbcS* and *G6PD*, featured prominently among genes found up-regulated in hairy vetch grown tomato leaves (Kumar et al. 2004). Interestingly, the promoters of these genes harbor the NIT2 element, which has been implicated in nitrogen regulation (Fu and Marzluf 1990).

N signaling is intimately associated with hairy vetch-grown tomatoes (Kumar et al. 2004; Mattoo and Abdul-Baki 2006). Is N the only contributing factor in legume cover crop-mediated enhancement of longevity

and defense properties of the subsequent crop? In their molecular analysis, Kumar et al. (2004) did not find up-regulation of senescence-associated protein (*SAG12*) or the nitrate transporter *CHL1*, whose transcripts were found over-expressed in plants that received short-term exposure to external nitrate concentrations (Wang et al. 2000). Similarly, the expression of an antifungal protein osmotin (Liu et al. 1994), which was found up-regulated in hairy vetch-grown tomatoes (Kumar et al. 2004), actually decreased by 2.5-fold in *Arabidopsis* exposed to high N levels (Wang et al. 2000). Thus, it would be simplistic to presume that N is the only driving element for the effects of legumes on crops. As discussed above, nutrient release in cropping systems based on input of organic residues relies on degradation processes that are likely to release many compounds in addition to the well-known macro- and micro-nutrients.

Legumes are known to produce a wide variety of secondary metabolites that like isoflavones have a health promoting effect. Likely, there are other factors present in legume foliage residue that are complementary with the subsequent crop and signal longer growth duration and enhance tolerance to disease/pests? Thus, GC-MS based metabolome analysis of the legume *Lotus* quantified nitrile glucosides, linamarin and lotaustralian cyanogenic glucosides, and terpenoids – compounds suggested to be involved in plant-insect interactions (Arimura et al. 2004; Forslund et al. 2004; reviewed by Udvardi et al. 2005). It is important to obtain an understanding of such interactive biology by investigating legume biology. The thrust for comparative genomics for model legumes including *Vicia faba*, *Lotus*,

Medicago and soybean is therefore a powerful approach to develop a comprehensive information on physiological, biochemical and genomic traits of legumes which should allow knowledge-based application for achieving agricultural goals (Udvardi et al. 2005; Domoney et al. 2006). Analysis of plant organs from diverse legume species and applying high-throughput methods of metabolomics, transcriptomics and proteomics should generate an understanding of legume biology principles and plant-plant interactions.

B. Other Nitrogen:Carbon Interactive Metabolites

Legumes interact with rhizobia and develop symbiotic nitrogen fixation in their nodules, a process that is predated by other plant development processes and evolved some 60 million years ago (see Jiang and Gresshoff 2002). This symbiosis that provides the plant with N and the soil rhizobia with carbon is now thought to be mostly a plant-controlled process (Caetano-Anolles and Gresshoff 1991; Kawaguchi et al. 2002). However, relatively more is known about the bacterial involvement of this symbiosis than about the plant genetics involved, because of the complexity of legume biology. The genome initiatives mentioned in the previous section should further our understanding of the legume genetics that has a direct impact on legume-rhizobia symbiosis.

During the legume-rhizobial interactions, the ureides allantoin and allantoic acid remain major nitrogenous products as well as polyamines that have been found to regulate a number of processes in plants. These and possibly other functional metabolites present in legume cover crops can be taken up by

the succeeding crop, transported from roots to other plant parts and subsequently influence tissue-specific gene regulation. Some microorganisms play a symbiotic role in not only fixing atmospheric N but also in producing factors that stimulate host plant growth (Steenhoudt and Vanderleyden 2000; Ma et al. 2002; Penrose and Glick 2003). Atkins et al. (1982) provided direct evidence for the transport of ureides and utilization of ureide-N in cowpea plants for the synthesis of amino acids and insoluble nitrogen-containing compounds using ^{15}N and ^{14}C feeding studies. This study suggested that ureides can be transported via phloem upward to fruits or downward to the roots of the plant, and also freely exchanged from xylem to phloem. Therefore, they concluded that ureides constitute a significant source of translocated nitrogen for protein synthesis in phloem-fed organs.

It is now realized that the phloem stream is a conduit for nucleic acids and proteins, some of them by their very nature can upon translocation regulate gene expression (Atkins and Smith 2007). Amides glutamine and asparagine as well as ureides or citrulline, depending on the species, predominate in xylem and represent translocated forms of assimilated nitrogen in nodulated legume roots (Atkins 1991). Further, Rhizobium-legume symbiosis also involves translocation of unique solutes including the plant hormone cytokinin that can modulate plant growth and development (Upadhyaya et al. 1991). It is becoming increasingly clear that xylem and phloem channels carry important molecules that when unloaded in a particular plant organ act as molecular signals. Studies with a pumpkin (*Cucurbita maxima*) phloem

RNA binding protein introduced into rice showed a root-ward protein mobility in rice sieve tubes. This occurs through transport systems that interact with other proteins suggesting protein-protein interactions in the phloem sap. In contrast, shoot-ward translocation involved passive bulk flow (Aoki et al. 2005).

A critical role for purine catabolism with concomitant accumulation of ureides in delaying leaf senescence has been presented (Brychkova et al. 2008a). That ureides play an important role in dark and senescence-induced purine remobilization was unmasked in the *Arabidopsis* mutant developed to silence a key gene in ureide biosynthesis pathway, xanthine dehydrogenase (*Atxdh1*) (Yesbergenova et al. 2005; Brychkova et al. 2008b). The ureides were shown to serve as reactive oxygen scavengers as well as favorable N:C compounds. These studies provide a new paradigm for developmental senescence.

Polyamines are nitrogen-rich compounds with anti-senescence property and capacity to scavenge reactive oxygen species (Kaur-Sawhney and Galston 1991; Borrell et al. 1997; Mattoo and Handa 2008). The most common plant polyamines include the di-amine putrescine, tri-amine spermidine and tetra-amine spermine. Pre-treatment of cucumber cultivars with spermidine and spermine before exposure to chilling stress was found to inhibit cold-induced lipid peroxidation, and NADPH oxidase was suggested to be the likely target (Shen et al. 2000). Later, Cuevas et al. (2004) reported that polyamines modulate NADPH oxidase in *Lotus glaber*. These and other studies suggest that polyamine metabolism and action respond to oxidative stress in

legumes and other plants. Studies on transgenic tomato engineered to have fruit-specific accumulation of spermidine and spermine have shown that these polyamines revive anabolic processes, signal N:C interactions and markedly impact fruit metabolism and gene expression (Mattoo et al. 2006,2007; Mattoo and Handa 2008; Neelam et al. 2008). The fruit that accumulated spermidine and spermine were nutritionally enriched, had higher juice quality and with improved organoleptic characteristics (Mehta et al. 2002; Mattoo et al. 2006). Interestingly, hairy vetch mulch grown tomato plants produced more spermine in the fruit than that from plants grown under conventional, black polyethylene (Neelam et al. 2008). Very little is known about polyamine transporters, particularly in plants. The protein product of the *PuuA* gene cluster in the bacterium *Escherichia coli* was studied and found to catalyze γ -glutamylation of putrescine (Kurihara et al. 2008). *PuuA* was found to have a high K_m for putrescine, in millimolar levels, which is consistent with the high (12 mM) levels of putrescine that *E. coli* can accumulate.

Mechanisms that allow plants to sense and respond to changes in C:N ratio are emerging (Smeekens 2000; Hellmann et al. 2000; Vidmar et al. 2000; Coruzzi and Zhou. 2001; Mattoo et al. 2006). These multiple C and N signals can serve as effective tools to understand how different sensing pathways cross talk with one another and send long distance signals to regulate plant growth, development and senescence.

C. Legume-Arbuscular Mycorrhizal Fungus Interactions

Apart from the root-nodule symbiotic relationship of leguminous plants with N-fixing rhizobia, most higher plant roots associate with the arbuscular mycorrhiza fungi (AMF), an association by which plants can acquire phosphate for growth (Smith and Read 1997). Both these associations involve genetic interactions via signaling molecules, for instance, the Nod factors that signal reprogramming of root development (Oldroyd 2001; Kistner and Parniske 2002). Two genes, *CASTOR* and *POLLUX*, have been shown to be among the determinants of microbial-plant root symbiosis since mutants of these genes in *Lotus japonicus* affect symbiosis with arbuscular mycorrhiza and, independently, root nodulation process (Ehrhardt et al. 1996; Novero et al. 2002; Harris et al. 2003). Both genes encode proteins that are localized in root plastids and have been shown to be essential for early signal transduction events such as calcium spiking that leads to successful endosymbioses (Imalzumi-Anraku et al. 2005). These studies concluded that “an ‘ancient’ endosymbiont helps bacterial and fungal ‘newcomers’ to infect their partner.”

In addition to helping plants to acquire phosphorus from the soil (Harrison and Van Buuren 1995), AMF can also acquire and transfer nitrogen to the host plant (He et al. 2003). In an elegant study, Govindarajulu et al. (2005) used stable isotope labeling to show that inorganic nitrogen taken up by AMF located outside the roots is recovered in amino acids, then moved as arginine to the intraradical mycelium, and from there transferred to the plant without carbon. These flux events were consistent with the expression of N assimilation genes in the extraradical tissue and arginine catabolism genes in

the intraradical mycelium (Govindarajulu et al. 2005). The fact that the AMF use arginine as the N carrier is advantageous because of its property to bind polyphosphate (Martin 1985). It has been suggested that polyphosphates are the P form translocated by AMF (Smith and Read 1997), thus enabling AMF to transfer nitrogen simultaneously with phosphorus to the plant roots. For such a scenario to function well, plant roots should be able to metabolize arginine polyphosphates and use them as an alternative energy source for plant growth and development. Also, such endosymbiotic relationships may be significant for enhancing multiple nutrient cycling within an ecological and physiological context.

In an exciting breakthrough, studies with pea (*Pisum sativum* L) *ccd8* mutant (Gomez-Roldan et al. 2008) and rice *d* mutant (Umehara et al. 2008), deficient in carotenoid cleavage dioxygenase (*ccd*), have revealed the significance of a group of terpenoid lactones, strigolactones, in AMF-plant symbiosis. Strigolactones are root-synthesized molecules that interact with AMF and promote nutrient uptake by plants. These properties as well as their roles in seed germination and shoot branching across the plant kingdom have prompted suggestions to include strigolactones as new plant hormones (Gomez-Roldan et al. 2008; Umehara et al. 2008).

It is therefore clear from this discussion that the metabolic function of a legume plant is defined by root-nodule and root-AMF interactions and that these processes should be important considerations in future experimentation for understanding the mechanism(s) and synergism between cover crops and the subsequently grown crop.

D. Molecular Signature of Hairy Vetch -Grown Tomato

A window into the black box of genetic and biochemical changes associated with the phenotypic characteristics of tomato plants grown in hairy vetch mulch was opened by a molecular analysis aimed at studying differential gene expression in leaves of plants grown in hairy vetch versus those grown in the conventional, black polyethylene (Kumar et al. 2004). Surprisingly, a select transcript signature pattern was evident in the leaves of the hairy vetch-grown tomatoes. This gene signature comprised: N-responsive genes such as *NiR*, *GS1*, *rbcl*, *rbcS*, and *G6PD*; chaperone genes such as *hsp70* and *BiP*; defense genes such as chitinase and osmotin; a CK-responsive gene, *CKR*; and *GA₂₀* oxidase. The transcripts of these genes were at a higher steady-state level in the hairy vetch-grown tomato foliage (Fig. 3). The transcript signature pattern paralleled protein profiles for photosynthesis proteins – small and large Rubisco subunits, glutamine synthetase-1; defense-related proteins - chitinase and osmotin; and chaperone proteins - heat shock protein-70 and binding protein BiP. Higher and durable accumulation of Hsp70 and BiP transcripts in HV-grown tomato is an indication of their recruitment in keeping the anabolic machinery functional, thereby increasing the lifespan of these plants. Thus a coordinated molecular basis seems responsible for the phenotypic characteristics observed in these plants: plants live longer, have delayed foliar senescence and are more tolerant to foliar diseases. Over-expression of cytosolic GS-1 in transgenic tobacco was previously shown to lead to an improved growth phenotype (Oliveira et al. 2002). Similarly, BiP over-expression in

transgenic tobacco results in alleviating endogenous oxidative stress (Alvim et al. 2001). Further validation comes from experiments showing that hairy vetch residue taken from the field imparts the delayed senescence phenotype to tomato plants when grown in the greenhouse (Kumar et al. 2005). Interestingly, Lu et al. (2005) demonstrated that the type of N fertilizer, organic versus inorganic, used to grow wheat can bring about a differential gene expression response. Likewise, tomato fruit responds in a specific manner in regulating gene expression in response to accumulation of organic N in the form of polyamines (Mattoo and Handa 2008; also see below).

Differential transcript expression profiles for hormone signaling genes - auxin-responsive *ACS6*, GA_{20} oxidase, and *CKR* (Fig. 4) are yet another hallmark of hairy vetch-grown tomatoes, implicating gibberellin (GA) and cytokinin (CK) signaling in delayed foliar senescence and enhanced disease tolerance in HV-grown plants. CK regulates a myriad of processes in plant growth and development including a role as an anti-senescence hormone (Nooden et al. 1979) and an N signaling molecule (Sakakibara et al. 1998; Takei et al. 2001). Initiation of senescence in plant organs is concomitant with a decrease in CK signaling (Hwang and Sheen 2001; Inoue et al. 2001). A direct correlation between the CK level and retention of greenness was demonstrated by expressing the *Agrobacterium* CK biosynthesis gene, *tmr*, in tobacco leaf (Smart et al. 1991). Interestingly, engineered expression of bacterial CK biosynthesis genes in tobacco plants that caused accumulation of CK led to induction of several defense-related genes including chitinase (Memelink et

al. 1987) and osmotin (Thomas et al. 1995).

Slight but a significant increase in GA_{20} oxidase transcript levels in hairy vetch-grown tomato foliage, compared to that grown in black polyethylene, raises the possibility that GA also directly, or through cross talk with CK, contributes to differential gene regulation in tomatoes cultivated in the hairy vetch mulch. Additional evidence for differential hormonal signaling in tomato plants cultivated in the two mulch systems is also exemplified by up-regulation in the black polyethylene-grown plants of *ACS6*, a key gene in the biosynthesis of the aging hormone ethylene (Fluhr and Mattoo, 1996), which is also inducible by the hormone auxin (Yoon et al. 1999). Coincident with early and higher accumulation of *ACS6* transcripts in the black polyethylene-grown tomato leaves is the accumulation of cysteine protease transcripts, an additional senescence-associated gene. The simultaneous increase in cysteine protease and *ACS6* transcripts may not be a mere coincidence. Mataraso et al. (2005) have found that a cysteine protease-like protein binds to the -715 to -675 promoter region of a related tomato ACC synthase gene, *ACS-2* gene. They further found that over-expression of the cysteine protease-like protein in transgenic plants harboring the GUS reporter gene under the control of the *ACS2* promoter results in the activation of the GUS gene. Thus, early and sustained accumulation of cysteine protease transcript in tomato plants grown under black polyethylene mulch could activate ethylene biosynthesis by induction of ACC synthase transcripts, thereby promoting senescence in these

plants earlier than in the hairy vetch-grown ones.

Signaling pathways tuned to hormonal cues seem well coordinated in the hairy vetch-tomato system (Kumar et al. 2004; Mattoo and Abdul-Baki 2006), and a detailed molecular examination of such interactions should reveal new insight into regulation of distinct sets of genes in tomato plants that are involved in the fitness of plants and tolerance to diseases. In this context, it is interesting to note that a role for the CK-signaling pathways has been suggested in plant-microbe interactions involving rhizobacteria (Ryu et al. 2003).

E. A Working Model Explaining Hairy Vetch-Tomato Interactions

The select transcript/protein signature pattern allowed developing a model (Fig. 5) to explain how hairy vetch system may direct beneficial attributes in tomato (Kumar et al. 2004). Features of this model are in consonance with the scheme proposed by Sugiyama and Sakakibara (2002) on N sensing, CK accumulation and transcription of N-responsive genes. Hairy vetch based soil management influences root physiology as well as causes differential hormonal signaling. A robust root growth habit having larger spread of adventitious roots compared to tomato plants grown on black polyethylene (Sainju et al. 2000) favors CK synthesis, thereby enabling more CK available from the root to the shoot. The CK signal would be transduced through the His-Asp phospho-relay system, inducing the transcription of N-responsive genes (Imamura et al. 2003). Does CK level signal leaf longevity as well as defense against pests in HV-grown tomatoes? Elevation of the cytokinin receptor kinase CKR is interpreted to mean that a

continued influx of CK into the leaf occurs (see also Papon et al. 2002). Upon shoot-ward transport of CK, it is perceived at the leaf membranes and enters the cellular pool, in turn signaling processes that keep the leaf from senescing. It can also form a tripartite complex with basic chitinase and osmotin, both of which bind cytokinins in tobacco callus (Kobayashi et al. 2000). As a result of the tripartite combination of CK, basic chitinase and osmotin, the two defense proteins remain stable for a longer duration, which, in turn, keeps the level of free CK to a minimum. This sequestration of CK can achieve the objective of preventing feedback (autoregulatory loop) signaling from the shoot to the root by high free CK levels, and, thereby, allow for continuous flow of CK from the root to the shoot. Also, chitinase and osmotin proteins can bind actin and cause cytoplasmic aggregation, and thereby participate in pathogen defense, as in potato cell suspensions (Takemoto et al. 1997). The high level of endogenous co-expression of chitinase and osmotin transcripts in HV-grown tomatoes likely contributes to disease resistance (Kumar et al. 2004). This was validated by studies showing sheath blight resistance in rice engineered to co-express chitinase-osmotin double construct (Kalpana et al. 2006). Engineering resistance to a number of fungi has been broadened by introducing more than a single defense gene: chitinase-glucanase combination reduced lesion development in tobacco by *Cercospora nicotianae* (Zhu et al. 1994), in tomato by *Fusarium oxysporum* (Jongedijk et al. 1995), in carrot by different *Alternaria* sps. and *Erysiphe heraclei* (Melchers and Stuijver 2000), and in rice by *Rhizoctonia solani* (Sridevi et al. 2008).

F. Genotype × Environment and N:C Interactions

Conventional methods of selection and breeding in the last century coupled to fertilizer and pesticide use, improved irrigation and integrated pest management led to increased crop production and contributed to Green Revolution. Recent advancements have utilized molecular markers to assist in the selection process while technological innovations such as genetic engineering and biotechnology have provided new knowledge about genes and their function at the cellular and molecular levels (Chrispeels et al. 2002; Razdan and Mattoo 2005, 2007). Environmental impact data obtained from 42 field experiments with Bt cotton and maize have verified that genetically modified crops can contribute to sustainable agriculture (James 2005, 2007; Marvier et al. 2007). In light of these advances, it is imperative that genetically engineered crops be developed to be compatible with alternative agricultural practices and to learn how the two interact to influence plant growth in the field, fruit metabolism, and overall agricultural sustainability.

A transgenic tomato line (ySAMdc line 579HO; Mehta et al. 2002; Mattoo et al. 2006) engineered to accumulate polyamines in a fruit-specific manner was field tested alongside the azygous control line (556AZ; Mehta et al. 2002; Mattoo et al. 2006) in hairy vetch mulch and conventional black polyethylene. This study that profiled twenty fruit metabolites such as amino acids, sugars and organic acids and expression patterns of a number of genes demonstrated that growth environments created by using hairy vetch mulch or black polyethylene influence the gene

expression of a plant (tomato genotypes) in a unique manner, and exemplified genotype X mulch-dependent interactions on fruit phenotype (Neelam et al. 2008). Since hairy vetch stimulated spermine accumulation in the non-transgenic fruit, a feature genetically enabled in the 579HO fruit by the ySAMdc transgene (Mehta et al. 2002) when grown in black polyethylene, these data suggested a linkage between polyamines and metabolite content in tomato fruit.

Notably, synergism was found between hairy vetch mulch and transgenic tomato in upregulating N:C indicator genes PEPC and ICDHc in the fruit. Hairy vetch increases CKR transcripts (Kumar et al. 2004) also in the fruit (data not shown), suggesting that polyamines, in concert with N and CK, orchestrate the N:C metabolism in tomato fruit. The mulch-dependent and transgene-dependent changes in fruit metabolism occurred without any apparent qualitative deviation from normal fruit metabolites (Neelam et al. 2008). This observation bodes well for the integration of genetically engineered (transgenic) crops with ecologically-based agriculture practices. Given more precise knowledge of the molecular interactions within agroecosystems, a diversity of crop genotypes may be designed with suites of genes that are adapted to local ecological management systems each with unique ecological requirements and constraints.

IV. AN INTEGRATED APPROACH TO SUSTAINABLE HORTICULTURE

Twentieth century agriculture was characterized by the development of agricultural products for fertilizing crops and controlling weeds, pests, and

diseases as well as an industry for economically producing and marketing these products. These products could be targeted to very specific requirements including delivering targeted ratios of nutrients, selective control of specific weed or pest species without injuring associated crop species, and plasticized materials for favorably altering crop environmental conditions. Use of these products provided an unprecedented level of consistency for optimizing crop yields and eliminating detrimental influences of weeds, pests, and diseases. However, rising energy costs threaten to undermine the cheap raw materials from which these products are manufactured as well as the transportation for delivery to the farm gate. In addition, issues relating to the environmental hazards associated with use of selected products on farm and during the manufacturing process heighten interest in discovering alternative approaches. In this review we have highlighted ecological and genetic approaches that are likely to contribute toward defining future agricultural alternatives.

The challenge will be to synthesize knowledge of genetic/metabolic systems with knowledge of agroecosystem structure and function to understand how manipulation and control of specific gene expression will translate into directing processes at the ecological scale. Rapid advances in technology for modifying crop genetic profile and expression will aid in creating plants with traits most adapted to cropping systems based on sustainable ecological management principles. For example, expression of the gene encoding terpene synthase 23 that produces volatile terpenes that attract entomopathogenic nematodes and /or parasitic wasps in

response to damage by rootworms or leaf damaging larvae, respectively, has been bred out of modern maize cultivars (Köllner et al. 2008). Restoring this genetic function to maize would enhance the resistance of these lines to both above and below ground pest damage in conjunction with ecosystem management that provides a suitable habitat for populations of the required entomopathogenic nematodes and parasitic wasps. Thus, solutions would involve both an understanding of genetic mechanisms as well as the appropriately compatible ecosystem management.

The hairy vetch-tomato model system described above is a composite of two major systems, each of which is interlaced with symbiotic associations, as illustrated in Fig. 5. In System 1, interactions of live hairy vetch roots with rhizobia and AMF upload the vetch foliage with functional primary and secondary metabolites. These metabolites remain in the foliage residue until released to become the substrate and signaling molecules for System 2 interactions between the hairy vetch residue and succeeding tomato plant growth processes. The latter System is characterized by a dynamic equilibrium, at a minimum, between longevity and disease resistance genes enabling a more productive and fit tomato plant within the agroecosystem. Whether legume cover crops with a high N/C ratio, in general, create a universal signaling system controlling ecosystem interactions with succeeding crop species needs to be investigated. But we advocate that multidisciplinary research between crop ecologists and molecular biologists is needed to better understand these linkages between molecular mechanisms and whole plant function within the context of the agroecosystem.

Resulting information will serve to refine agroecosystem management and to direct development of improved crop genetics. Although few current agricultural ecologists and molecular biologists are trained to engage in integrated research of this type, we encourage educational programs to promote this type of interdisciplinary training in the future.

The synergy between on-farm produced organic inputs and field production of genetically engineered, value-added crops such as tomato is an important step toward future sustainability of horticultural produce. It will be of interest to discover the nature of synergy between other nutritionally enhanced plants including fruits and vegetables (Shintani and DellaPenna 1998, Valpuesta 2002) and appropriate leguminous cover crop production systems. Integrating genetically modified crops with sustainable agricultural practices would mitigate the impact of intensive practices on environment and simultaneously address the issues of crop productivity, protection and quality. Such a paradigm for sustainable agriculture provides a system that decreases the disadvantages of conventional agriculture and increases environmental congeniality and economic viability of future agriculture. It shifts the current paradigm toward sustaining future food production and addresses the opportunity of a 'second paradigm' (Sanchez 1994, reviewed by Uphoff 2006) that relies on new germplasm that is adaptable to adverse soil conditions, enhanced soil biological activity, and efficient use of nutrient cycling with minimal external inputs.

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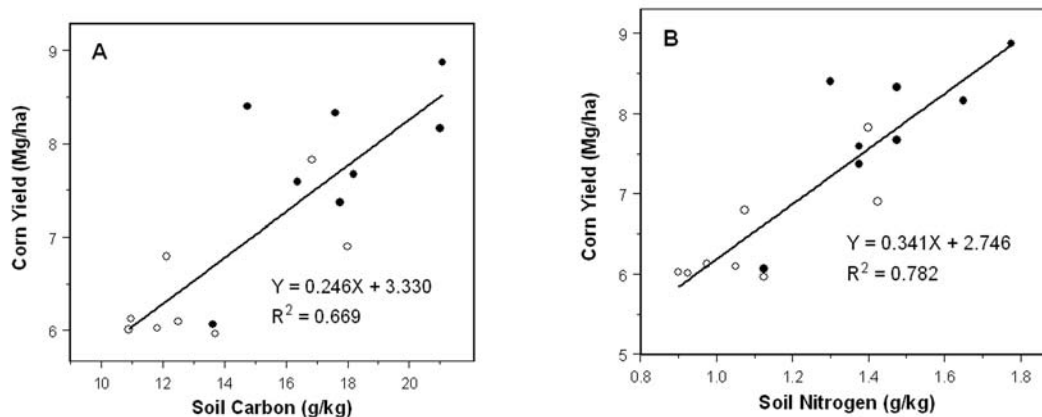


Fig. 1. Maize yield as a function of total soil carbon (A) or nitrogen (B) in a uniformity trial following 9 years comparison of reduced-tillage organic (solid symbols) and conventional no-tillage (open symbols) systems. Data is from Teasdale et al. (2007).

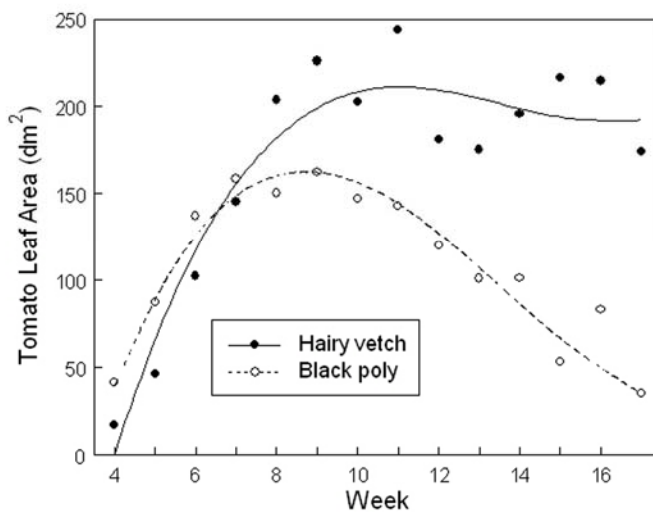


Fig. 2. Extended duration of tomato leaf area when grown in a hairy vetch versus black polyethylene mulch. Week 10 designates the beginning of fruit harvest. Leaf area duration of tomatoes in hairy vetch equaled 2259 dm²week⁻¹ compared to 1486 dm².week⁻¹ in black polyethylene. Data is from Teasdale and Abdul-Baki (1997).

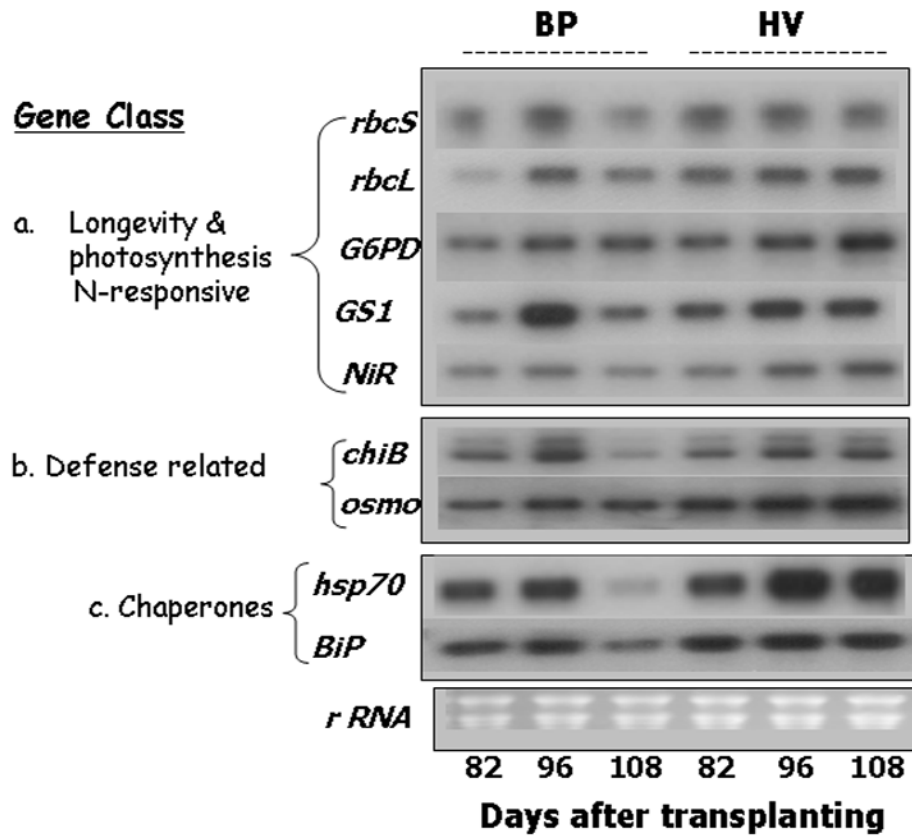


Fig. 3. A gene transcript expression signature revealed in hairy vetch (HV) grown tomato leaf in comparison to plants grown in black polyethylene (BP). Shown are the gene classes and respective northern blot analysis of total RNA from BP and HV grown tomato leaves harvested on the indicated days after planting. Modified after Kumar et al. (2004).

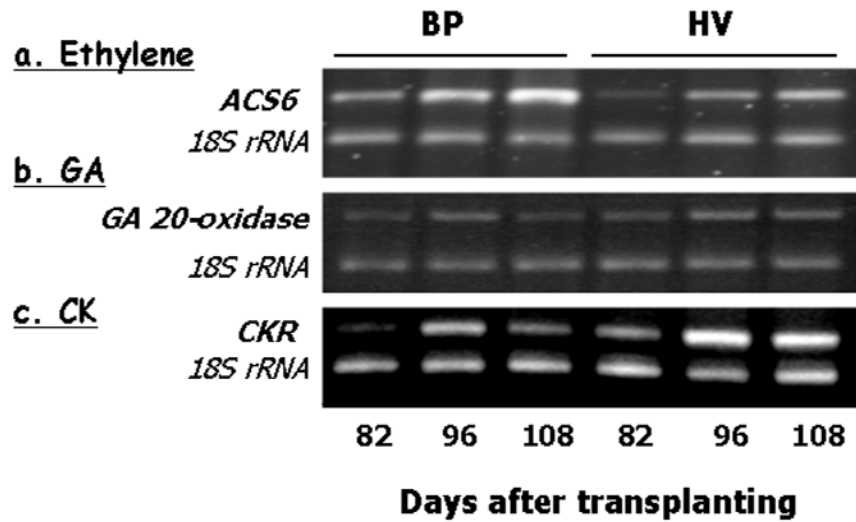


Fig. 4. Differential hormonal signaling highlighted in hairy vetch (HV) grown tomato. Real time PCR analysis showing expression patterns for IAA responsive ethylene biosynthesis gene (*ACS6*), GA signaling gene (*GA20 oxidase*), and cytokinin receptor kinase gene (*CKR*) in BP and HV grown tomato leaves harvested on the indicated days after planting. Adapted from Kumar et al. (2004).

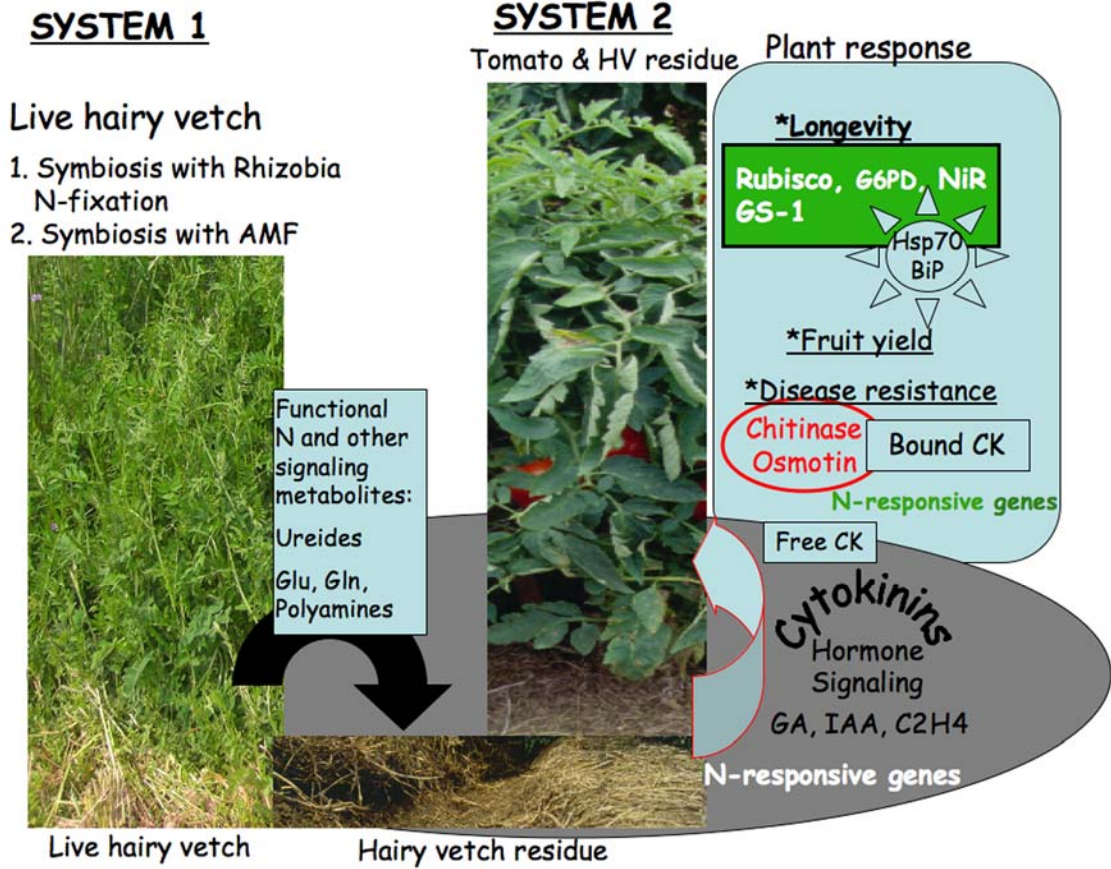


Fig. 5. A model illustrating the concept of two systems working in unison resulting in enhanced longevity, disease resistance and higher fruit yield in tomato plants grown in hairy vetch residue. See text for details.