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REVIEW ARTICLE

Plant-Soil Feedbacks and Soil Sickness: From Mechanisms to Application in Agriculture

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Abstract Negative plant-soil feedbacks play an important role in soil sickness, which is one of the factors limiting the sustainable development of intensive agriculture. Various factors, such as the buildup of pests in the soil, disorder in physico-chemical soil properties, autotoxicity, and other unknown factors may contribute to soil sickness. A range of autotoxins have been identified, and these exhibit their allelopathic potential by influencing cell division, water and ion uptake, dark respiration, ATP synthesis, redox homeostasis, gene expression, and defense responses. Meanwhile, there are great interspecific and intraspecific differences in the uptake and accumulation of autotoxins, which contribute to the specific differences in growth in response to different autotoxins. Importantly, the autotoxins also influence soil microbes and *vice versa*, leading to an increased or decreased degree of soil sickness. In many cases, autotoxins may enhance soilborne diseases by predisposing the roots to infection by soilborne pathogens through a direct biochemical and physiological effect. Some approaches, such as screening for low autotoxic potential and disease-resistant genotypes, proper rotation and intercropping, proper soil and plant residue management, adoption of resistant plant species as rootstocks, introduction of beneficial microbes, physical removal of phytotoxins, and soil sterilization, are proposed. We discuss the challenges that we are facing and possible approaches to these.

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Introduction

Plant-soil legacy-effects or feedbacks, the net effects of all positive and negative interactions between plant and soil organisms, have received increasing attention as a mechanism involved in many ecological phenomena such as plant invasion, species dominance, old-field succession, and soil sickness (Kardol et al., 2006; Bever et al., 2010; van de Voorde et al., 2012). Plants can influence soil organisms via the supply of organic matter, or rhizodeposition and soil organisms, in turn, can alter plant performance through mutualistic interactions, nutrition availability, or pathogenic activity, etc. In ecosystems, plants can modify the soil by root exudation, root deposition, and susceptibility to enemies and symbionts. These changes can increase or decrease subsequent plant growth, which is usually called positive and negative plant-soil feedback, respectively (Kulmatiski et al., 2008). Meanwhile, aboveground and belowground herbivores of preceding plants can induce changes in the soil biota, which greatly influence secondary metabolite accumulation, biomass, and aboveground multitrophic interactions of succeeding plants (Kostenko et al., 2012).

Soil sickness is a typical negative plant-soil feedback with a reduction in crop yield and a prevalence of soil borne diseases when the same crop or its related species are cultivated on the same soil successively. The problem of soil sickness dates to the beginning of agriculture, and in an ecological sense, to much earlier times. Theophrastus (ca. 300 BC), the father of Botany, wrote of how chickpea "exhausts" the soil and destroys weeds in his botanical works. In an ancient Chinese book, Jiminyaoshu (ca. 540) gave a detailed description of the importance of a cropping sequencing for high crop productivity. Later, many agriculturists and biologists investigated the involvement of autotoxic substances in cropping systems (See Grodzinsky, 2006). However, scientific work was not initiated until the beginning of 20th century. Pioneering work by Schreiner and Reed (1907; Schreiner and Shorey, 1909; Schreiner and Sullivan 1909; Russell and Petherbridge, 1912) revealed the involvement of phytotoxins and detrimental microbes in soil sickness (Börner, 1960). Later, many biologists and agronomists attempted to isolate phytotoxic substances from plant tissues, root exudates, and soils, and this trend was especially significant in the 1950s–60s and 1980s–2010s. Many phytotoxic substances have now been isolated from plants, soils and rhizosphere (Table 1).

Since the 1960s, great progress has been made in agricultural science and technology. In many areas, traditional cropping systems with multi-crops have been replaced by monocropping with specific crops in many intensive agroecosystems. The shift of cropping systems changes the relationship of plant-soil feedbacks and ultimately influences plant growth and sensitivity to soilborne pathogens. At present, soil sickness becomes prevalent in the production of many annual crops with intensive monocropping, and it also affects trees and shrubs in orchards (apple, pear, grapes, etc.), coffee and tea plantations, where it causes replant problems for fruit trees and regeneration problems in natural forests (Rice, 1984; Chou, 1999; Caboun, 2005; Canals et al., 2005). Accordingly, understanding the mechanisms of plant-soil feedbacks in agroecosystems is an important step before we gain insight into the mechanism of soil sickness and solve the problem for the establishment of sustainable agroecosystems.

The occurrence of soil sickness varies with plant species and is easily influenced by the soil type and environmental factors. The reasons are complicated and have not been clearly defined. Early works were mainly focused on phytotoxins in the root exudates and litter and on an ion imbalance in the soil (Schreiner and Reed, 1907). Since the 1960s, many soil-borne pathogens have been characterized from the soils or roots, and they contribute greatly to soil sickness. A survey in Japan and China revealed that soil sickness in vegetable crops is attributable to (i) soil-borne pests followed by (ii) deterioration of soil physicochemical properties and (iii) allelopathy/autotoxicity (Komada, 1988; Ogweno and Yu, 2006). In agreement with these studies, domestic rare plants experience strong negative feedback when grown in monoculture as compared to invasive plants (Klironomos, 2002). Klironomos (2002) concluded that the negative feedback responses are pathogen-density dependent. Others have shown the feedback is associated with allelopathy (van de Voorde et al., 2012).

Autotoxicity and the Action Mechanism in Soil Sickness

Allelopathy is a biological phenomenon by which an organism releases one or more biochemicals to the environment that are directly or indirectly harmful or beneficial to other plants or microorganisms (Rice, 1984). The biochemicals involved with beneficial or detrimental effects on the target organisms are known as allelochemicals. Autotoxicity is a type of intraspecific allelopathy where a plant species inhibits the growth of its own or relatives through the release of toxic chemicals into the environment (Singh et al., 1999; Yu et al., 2000). Similar to other allelochemicals, autotoxins are released into the environment through leaf volatilization, leachation and root exudation of living plants, as well as decomposition of dead plant tissue (Singh et al., 1999).

Autotoxicity has been observed in both natural and manipulated ecosystems. In agroecosystems in particular, autotoxicity causes losses in crop yields, regeneration failure of forests, and replant problem in orchards (Singh et al., 1999). Monocropping of annual crops, such as rice, alfalfa, cucumber, tomato, corn, wheat, sugarcane, and beans like soybean and pea, is known to reduce performance and decrease yields over a period of time (Chou, 1999). Autotoxicity also is prevalent in perennial plants, such as strawberry, apple, peach, citrus, grapes, cherries, ginseng, and roses (Singh et al., 1999). Plant extracts, root exudates, and sometimes the water or organic solvent extracts of soils after planting with these crops are usually autotoxic, leading to a 20–50 % decrease in growth rate (Singh et al., 1999). Interestingly, the autotoxic potential for many plants is species-dependent. Takijima and Hayashi (1959) revealed that the nutrient solution after tomato culture was toxic to the tomato plants but not to rice plants and *vice versa*. Similarly, we observed that root exudates of cucumber plants were toxic to the cucumber plants but not to figleaf gourd plants (Yu et al., 2000; Ding et al., 2007). Moreover, the release of autotoxic substances is stage-dependent. For example, cucumber and tomato plants exude autotoxic substances at the reproductive stage, while pea plants exude autotoxic substances mainly at the vegetative stage (Yu and Matsui, 1994; Yu and Matsui, 1999). In addition, autotoxic potential also is influenced by genotypes, light, and nutrition levels in many crops (Pramanik et al., 2000).

Many compunds have been identified as autotoxins from plants, root exudates, and soils. These chemicals include simple water-soluble organic acids, aliphatic aldehydes, lactones, long-chain fatty acids, naphthoquinones, anthraquinones, phenols, benzoic and cinnamic acids, coumarins, tannins, terpenoids, steroids, alkaloids, cyanohydrins, sulfides, oil glycosides, purines and others (Table 1). In fact, it is often quite difficult to isolate these substances from soils. Until now, several autotoxins have been isolated from

Table 1 List of known autotoxins

Plants	Autotoxic agents	Autotoxins	References
Alfalfa (*Medicago sativa*)	roots	medicarpin, 4-methoxy medicarpin, sativan, 5-methoxy sativan, coumarin, *trans*-cinnamic, salicylic, *o*-coumaric, chlorogenic and hydro-cinnamic acids	Miller et al., 1988; Dornbos et al., 1990; Chung et al., 2000; Chon et al., 2002
American ginseng (*Panax quinquefolium*)	roots	phenolic acids	He et al., 2009
Apple (*Pyrus malus*)	bark	phlorizin, phloretin, *p*-hydroxy hydrocinnamic, *p*-hydroxy benzoic acids, phloroglucinol	Börner, 1959
Asparagus (*Asparagus officinalis*)	roots	ferulic, iso-ferulic, malic, citric, fumaric and caffeic acids	Hartung et al., 1990; Miller et al., 1991
Broad bean (*Vicia faba*)	root exudates	lactic, adipic, succinic, malic, benzoic, vanillic, *p*-hydroxybenzoic, glycolic and p-hydroxyphenylacetic acids	Asaduzzaman et al., 2012; Asaduzzaman and Asao, 2012
Chininese fir (*Cunninghamia lanceolata*)	soil	coumarin, vanillin, isovanillin, *p*-hydroxybenzoic, vanillic, benzoic, cinnamic and ferulic acids, friedelin	Kong et al., 2008
Citrus (*Citrus sp.*)	bark	homovanillic acid, seselin, xanthyletin, oil	Burger and Small, 1983
Coffee (*Coffea arabica*)	plant tissue	caffeine, theophylline, theobromine, paraxanthine, scopoletin, caffeic, coumaric, ferulic, *p*-hydroxybenzoic, vanillic, chlorogenic acids	Chou and Waller, 1980
Cucumber (*Cucumis sativus*)	root exudates	benzoic,myristic, cinnamic, *p*-hydroxybenzoic, 2,5-dihydroxybenzoic, 3-phenylpropionic, *p*-hydroxycinnamic, palmitic and stearic acids, *p*-thiocyanatophenol, 2-hydroxybenzothiazole	Yu and Matsui, 1994
Eggplant (*Solanum melongena*)	root exudates	cinnamic acid and vanillin	Chen et al., 2011b
Huangqin (*Scutellaria baicalensis*)	roots	baicalin	Zhang et al., 2010a; b; c
Lettuce (*Lactuca sativa*)	root exudates	vanillic acid	Asao et al., 2004a; b
Parsley (*Pastinaca sativa*)	volatiles	essential oils	Gog et al., 2005
Pea (*Pisum sativum*)	root exudates	benzoic, cinnamic, vanillic, *p*-hydroxybenzoic, 3, 4-dihydroxybenzoic, *p*-coumaric and sinapic acids	Yu and Matsui, 1999
Peach (*Prunus persica*)	bark	amygdalin	Patrick, 1955; Patrick and Koch, 1958
Rehmannia (*Rehmannia glutinosa*)	soils	phenyl aromatic acids	Li et al., 2012
Rice (*Oryza sativa*)	plant decomposition	*p*-coumaric, *p*-hydroxy benzoic, syringic, vanillic, ferulic and *o*-hydroxy phenyl acetic acids	Chou and Lin, 1976
Schrenk's Spruce (*Picea schrenkiana*)	needles	3,4-dihydroxyacetophenone	Ruan et al., 2011
Strawberry (*Fragaria×ananassa*)	root exudates	lactic, benzoic, succinic, adipic and *p*-hydroxybenzoic acids	Kitazawa et al., 2005
Taro (*Colocasia esculenta*)	root exudates	lactic, benzoic, *m*-hydroxybenzoic, p-hydroxybenzoic, vanillic, succinic and adipic acids	Asao et al., 2003
Tea (*Camellia sinensis*)	soil	phenolic acids	Cao et al., 2011
Tomato (*Solanum lycopersicum*)	root exudates	4-hydroxybenzoic, vanillic, phenylacetic, ferulic, 2-hydroxy-3-phenylpropanoic caffeic acids	Yu and Matsui, 1993
Wheat (*Triticum aestivum*)	straw residues	ferulic, *p*-coumaric, *p*-hydroxybenzoic, syringic and vanillic acids	Guenzi and McCalla, 1966; Lodhi et al., 1987

nutrient solutions after hydroponic culture with the aid of adsorbents such as Amberlite XAD or activated charcoal. In cucumber and tomato, plant growth has been improved when the nutrient solution was supplied with adsorbents (Yu et al., 1993; Yu and Matsui, 1994). From the adsorbents, several benzoic and cinnamic acids with growth-inhibiting activity have been identified (Yu and Matsui, 1993, 1994). Autotoxins can impact many physiological and biochemical reactions (Fig. 1), a subset of which are discussed in detail below.

Cell Division The normal cell-cycle mode is characterized by a round of DNA replication (S phase) followed by mitosis and cytokinesis (M phase) and separated by two gap phases (G_1 and G_2). Cyclin-dependent kinases (CDKs) and their cyclin partners regulate the G_1/S- and G_2/M-phase transitions and the progression through and exit from the cell cycle. Work in our laboratory and others has established that root exudates, water extracts of roots and the identified autotoxins, such as cinnamic acids of cucumber plants,

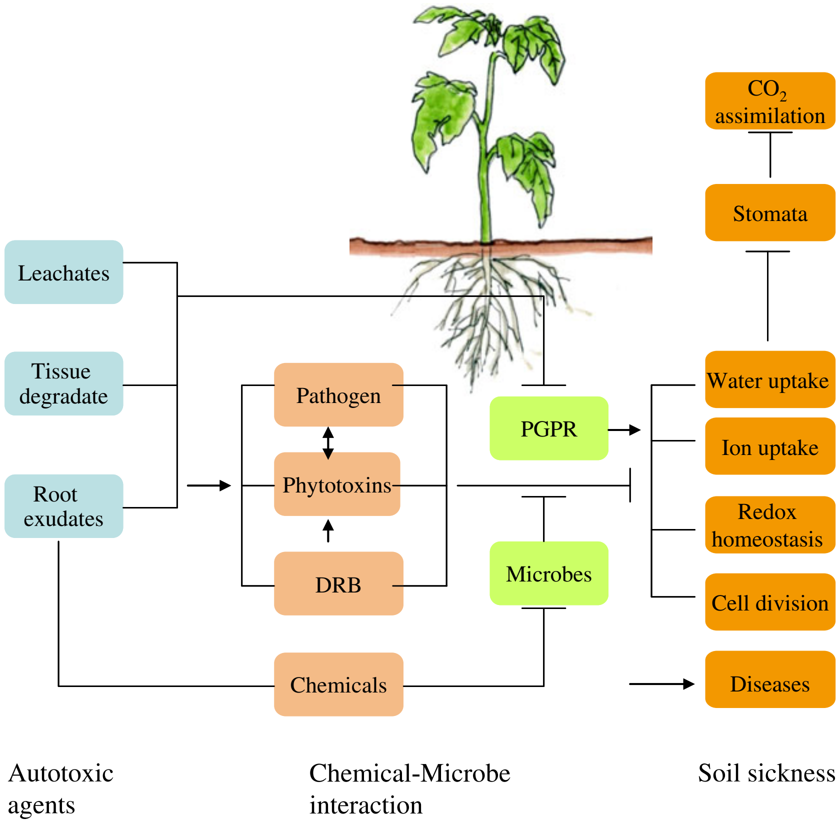

Fig. 1 Autotoxicity, autotoxin-microbe interactions and the soil sickness process. Chemicals: inorganic fertilizers and pesticides; DRB: deleterious rhizobacteria; PGPR, plant growth-promoting rhizobacteria

inhibit both cell proliferation and DNA synthesis in the root apical meristem, and this is accompanied by decreased transcripts of cell cycle-related genes and end reduplication (Zhang et al., 2009, 2010a).

Disturbed Water Relations and Ion Uptake Roots play a major role in plant growth and development. Root exudates and the constituting autotoxins can disturb cell membrane function in roots. The lipophilicity of benzoic and cinnamic acids is well correlated with the inhibition of ion uptake and subsequently root elongation in cucumber (Yu and Matsui, 1994). Additionally, many autotoxins and allelochemicals can inhibit the membrane H^+-ATPase activity that drives the uptake of essential ions, other solutes and water (Ye et al., 2004, 2006). Accordingly, decreased transpiration rate and ion uptake frequently are observed in plants after exposure to autotoxic agents.

Inhibition of Photosynthesis Decreased CO_2 assimilation and PSII electron transport efficiency have been observed in plants exposed to autotoxic agents. Some allelochemicals or autotoxins are inhibitors of electron transport at PS II; however, the effect is likely limited to the germinating seedlings, as the autotoxins are barely transported to the shoots of adult plants (Dayan, 2006). Significantly, exposure to autotoxins usually induces stomata closure, which may decrease the CO_2 availability and subsequently decrease CO_2 assimilation (Yu et al., 2003; Ye et al., 2006). Accordingly, it is possible that decreased PS II efficiency stems from a water-stress-induced decrease in CO_2 assimilation, which is a down-stream regulation mechanism in photosynthesis.

Interruption of Dark Respiration and ATP Synthesis In many cases, autotoxins have a more significant effect on germinating seeds than on older plants. As a metabolic process associated with the generation of ATP, respiration is one of the prominent processes in seed germination and also is sensitive to many autotoxins and allelochemicals. Recently, we reported that autotoxins such as cinnamic acid, which is found in the root exudates of cucumber, decreased the total respiration rate but increased the KCN-resistant respiration rate, thus suggesting an adaptation mechanism to avoid over-generation of reactive oxygen species (ROS) (Zhang et al., 2010b).

Redox Homeostasis and Defense Response There are increasing reports of ROS metabolism in plants after exposure to autotoxins and allelochemicals. In many cases, an over-generation or accumulation of ROS may induce damage to enzymes, lipids, DNA, proteins, and lipid peroxidation. However, it also is possible that ROS in cells after exposure to autotoxins functions as s signaling component in the allelopathic response. Like other stimuli, autotoxins may be perceived first by receptors on the cell membrane and then transduced downstream, resulting in a generation of secondary messages that include calcium ions (Ca^{2+}), ROS, and inositol phosphate (Yu et al., 2009). Accordingly, ROS and associated changes in $[Ca^{2+}]_{cyt}$ may be one part of the defense cascade in an autotoxic response. In cucumber, cinnamic acid induces NADPH oxidase-dependent H_2O_2 generation at the apoplast (Yu et al., 2009), which works as a secondary signal in response to many stimuli and induces an increase in the activity of many antioxidants, such as Cu/Zn-superoxide dismutase (Cu/Zn-SOD), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR), and non-enzymatic antioxidants, such as ascorbate and glutathione. However, the signaling role of ROS in the autotoxic response has not been well established until recently.

The Role of the Soil Microbial Community in Soil Sickness

Soil contains a vast diversity of microorganisms, and these microorganisms are critical to many of the biological, chemical, and physical processes that drive terrestrial ecosystems. Microbial diversity is important for soil quality and may be influenced by soil type, plant history, and agricultural practices, such as fertilization and pesticide application. Bacteria are the most abundant and diverse group of organisms in soil (Kennedy, 1999). For many decades, microbial communities have been monitored through traditional culture-dependent methods. Recently, culture-independent methods, such as fatty acid analysis (FAME and PLFA) and nucleic acid analysis (PCR-DGGE), have been widely used to estimate bacterial diversity (Theron and Cloete, 2000; Larkin, 2003; Wu et al., 2009). Some studies have shown that soil populations of culturable bacteria and overall microbial activity tends to be highest following barley, canola, and sweet corn rotations, and lowest with continuous potato, which is characterized by the greatest proportion of straight chain saturated fatty acids in soils under continuous potato growth (Larkin, 2003), while others have shown that soil microbial community functional diversity and genetic diversity (as indicated by RAPD markers) is decreased significantly by autotoxins such as cinnamic acid (Wu et al., 2009). Most recently, pyrosequencing of the bacterial 16S ribosomal RNA gene also has been used to characterize the bacterial community in the soil, rhizosphere and roots (Bulgarelli et al., 2012; Lundberg et al., 2012). Studies in Arabidopsis have revealed that soil type defines the composition of root-inhabiting bacterial communities, and that host genotype determines their ribotype profiles to a limited extent (Bulgarelli et al., 2012).

Plant community may change the soil microbial community by root exudation and root deposition, etc., Microbes may have beneficial, harmful, or neutral effects on plants (Sturz and Christie, 2003). The beneficial microbes include those that have direct or indirect positive effects on plant growth, mineral availability, and the stress response. For example, arbuscular mycorrhizal fungi (AMF) can improve plant resistance by improving phosphate acquisition and heavy metal resistance, while some microbial species can produce growth-promoting substances, such as indole-3-acetic acid and cytokinins (Khare and Arora, 2010). These microorganisms also function to inhibit or reduce the effect of soilborne phytopathogens, which is termed disease suppression (Garbeva et al., 2004). These microorganisms can suppress soilborne phytopathogens by niche competition, antibiosis, induced systemic resistance (ISR), and root camouflage (Sturz and Christie, 2003). The harmful or deleterious microbes include those that are phytopathogenic and those that produce phytotoxins. Several *Pseudomonas* spp. in monocropped soil are known for their ability to produce hydrogen cyanide (HCN) (Khare and Arora, 2010).

Root exudates vary with plant species, leading to changes in the soil microbial community. Roots of sorghum and maize exude strigolactones and benzoxazinoids that can stimulate AM fungi and attract *Pseudomonas putida*, a competitive colonizer of the maize rhizosphere with plant-beneficial traits, to the rhizosphere, respectively (Besserer et al., 2006; Neal et al., 2012). On the other hand, monocropping together with heavy applications of chemicals has been found to be accompanied by losses of soil biota and increased crop disease, e.g. potatoes (Carter and Sanderson, 2001). Studies have shown that soil microbial communities are changed after monoculture with a single plant species, e.g., peas, (Nayyar et al., 2009) and e.g., soybeans, (Li et al., 2010). Changes in soil biota will influence plant growth because soil biotas are involved in many processes important for plant growth and nutrition availability. In many cases, continuous monoculture reduces microbial competition in the root zone by lowering biodiversity among root-associated fungi and bacteria, thus enabling pathogenic populations to develop, thus increasing disease incidence and subsequent yield losses (Knops et al., 1999). Monocropping also results in the simplification of microbial structure, leading to decreases in the population of fluorescent *Pseudomonas fluorescence*, which is capable of producing the antifungal metabolite 2,4-diacetylphloroglucinol (Mazzola et al., 2002; Weller et al., 2002; Validov et al., 2005). For example, more than 60 % of the strains isolated from healthy soils corresponded to *Pseudomonas* sp., and 58 % of the isolates from sick soils were *Bacillus* sp., which is able to produce HCN *in vitro* (Benizri et al., 2005). Accordingly, yield reductions following the monoculture of a single crop species also is related to the accumulation of nonpathogenic, deleterious rhizobacteria (Schippers et al., 1987).

However, there also are quite different responses to monocropping. In contrast to sick soil or conducive soil, suppressive soil has a low level of disease development even though a virulent pathogen and susceptible host are present (Mazzola, 2002). In tomatoes, the suppressive characteristics are related to the microbial community (Shiomi et al., 1999). Interestingly, suppressiveness may be induced by continuous monocropping, intercropping, or short-term rotation with some genotypes, and this characteristic is attributed to the induction of specific fluorescent *Pseudomonas* genotypes with antagonistic activities toward this pathogen (Mazzola and Gu, 2000; Mazzola et al., 2001; 2002; 2004; Gu and Mazzola, 2003). However, it is unclear how the root exudates of these plants influence the microbial community and how the specific *Pseudomonas* population is related to the root exudates of these genotypes.

Interplay Between Autotoxins and Microbes in Soil Sickness

Soil is a complicated matrix, and soil sickness may stem from the interaction of different factors such as autotoxins, microbes, and others, that lead to growth inhibition and a prevalence of soilborne diseases. Plant-microbe interactions extend over time, space, and substrate. While root exudates influence the composition of microbial communities in the root zone, rhizobacteria themselves can change the composition of root exudation in plants and finally the products (Meharg and Killham, 1995). In addition, antagonism also occurs between microbes. The presence of deleterious rhizobacteria (DRB) may increase plant susceptibility to other pathogens (Fredrickson and Elliott, 1985). In fact, both enhancement and suppressive effects of microbial modification of autotoxins have been observed in many soil sickness phenomena. This interplay may partly explain the different responses of plants to specific autotoxins or allelochemicals in different types of soils.

Many plant-soil feedbacks are mediated by microbes in the soils. Autotoxicity in peach plants is attributed to amygdalin, which is broken down in the soil by microbes into toxic cyanide substances, causing injury to roots of young peach seedlings (Patrick, 1955). A similar phenomenon also has been observed in the soil sickness of walnut with juglone as the autotoxin (Thevathasan et al., 1998). In contrast, many allelochemicals or autotoxins are easily degraded by microbes (Blum, 1998; Blum et al., 2000; see also Weidenhamer et. al., 2013). In one study, several benzoic and cinnamic acids disappeared a few days after amending the soils (Blum et al., 2000). There is increasing evidence that autotoxins or allelochemicals can modify the prevalence of many soilborne diseases. Like root exudates, autotoxins or allelochemicals can change soil microbial genetic diversity, biological activity, and microbial metabolic activity, which alter soil microbial ecology and accordingly affect the growth of plants, with an accumulation of allelochemicals in the soil (Szabo and Wittenmayer, 2000; Wu et al., 2009). Research in our laboratory and in others has shown that root exudates of cultivars susceptible to Fusarium wilt stimulates spore germination and fungal growth, while resistant genotypes inhibited spore germination (Wu et al., 2006, 2010; Yu et al., unpublished). Declines in productivity in continuous monocultures of crops also are attributed to the synergistic interference of autotoxicity and soil-borne plant pathogens (Ye et al., 2006). In asparagus, autotoxic substances derived from its tissues not only depressed seedling emergence and reduced seedling growth but also increased *Fusarium* virulence (Hartung and Stephenes, 1983; Huang et al., 2000). Ginseng saponins (ginsenosides) present in the root exudates and the soil associated with the roots of American ginseng (*Panax quinquefolius* L.) stimulated the growth of soilborne pathogens of American ginseng (Nicol et al., 2003). Similarly, allelochemicals released by *Scutellaria baicalensis* negatively affected *S. baicalensis* directly, by inducing autotoxicity, and indirectly, by increasing pathogen activity in the soil (Zhang et al., 2010c). There also is evidence that exotic invasive plants accumulate native soil pathogens, which inhibit native plants (Mangla et al., 2008). Others, however, have shown that secondary metabolites, such as flavones, phenolics, and saponins, from the invasive *Solidago canadensis* L. accumulate in soil and inhibit the soil pathogen *Pythium ultimum* (Zhang et al., 2011).

Soil sickness is common in crops such as cucumber and watermelon. Cucumber plants have autotoxic potential by exuding substances, such as cinnamic acid (Yu and Matsui, 1994). These substances significantly increase ion leakage by increasing membrane permeability (Yu and Matsui, 1997) and by affecting the activity of ROS scavenging enzymes, such as peroxidase and superoxide dismutase (SOD) (Yu et al., 2003). Due to the sensitivity of cucumber to *F. oxysporum*. f. sp. *cucumerinum*, the pathogen of Fusarium wilt, and autotoxins (Yu and Matsui, 1997), it serves as a good experimental system to study the interaction between a soil-borne pathogen and an autotoxin. Exposure to cinnamic acid results in enhanced membrane peroxidation, decreased plasma membrane ATPase activity, and increased incidence of Fusarium wilt (Ye et al., 2004, 2006). Autotoxins enhance Fusarium wilt by predisposing cucumber roots to infection by soilborne pathogens through an indirect biochemical and physiological effect (Ye et al., 2004, 2006). It is likely that soil sickness results from an interaction of many factors, such as autotoxins and pathogens (Fig. 1).

Approaches to Overcome Soil Sickness

Although soil sickness is a complex phenomenon, it can at least partially be overcome by the integrating the following practices:

Screening for Low Autotoxic Potential and Disease-resistant Genotypes There are intraspecific variations in the autotoxic potential of many crops. Work on cucumber has revealed that many commercial cultivars have low autotoxic potentials, while others show strong potential (Asao T., personal communication). A series of genotypes with resistance to different soil-borne pathogens have been developed.

Adoption of Resistant Plant Species as Rootstocks Autotoxicity and pathogens are species–dependent in many cases. For example, root exudates of both cucumber and watermelon show high autotoxicity but not toxicity to other species, such as figleaf gourd (Yu et al., 2000). A recent study revealed that there was an interspecific difference in the uptake and the recognition of autotoxin(s) (Yu et al., 2009), which induced oxidative stress accompanied by root cell death in cucumber, an autotoxic plant, but not in figleaf gourd, a cucumber relative (Ding et al., 2007). Genotypes resistant to pathogens and autotoxins can be developed as rootstocks for many horticultural crops (Asao et al., 1999).

Proper Rotation and Intercropping A proper rotation can decrease pathogen populations and also minimize the autotoxic effects of the crops. The residues of crops like Brassicaceae and marigolds also can be useful in suppressing soilborne pathogens and nematodes (Cohen et al., 2005). Furthermore, the allelopathic properties of cover, smother, and green-manure crops, or crops grown in rotation can be useful for pest management (Singh et al., 1999; Farooq et al., 2011). Many crops exude nematicides and antimicrobial substances. For example, intercropping or rotation with Chinese chive can decrease the occurrence of bacterial wilt caused by *Pseudomonas solanacearum*, and the root exudates from Chinese chive plants exhibit strong inhibitory effects on the bacterial pathogen (Yu, 1999; Zhang et. al., 2013). Rotation with cereal crops such as sorghum and maize suppresses the incidence of nematode and other root diseases in tomato and cucumber (unpublished data). It remains to be determined, however, that whether strigolactones and benzoxazinoids in the root exudates of these crops such as maize contribute to their beneficial effects. It is, therefore, apparent that plant diversity is an important factor for successful plant growth in agroecosystems.

Proper Soil and Plant Residues Management Many crop residues release autotoxic substances and provide an environment suitable for the survival of soilborne pathogens. Removal of these residues from the soils may be an important step for overcoming soil sickness (Singh et al., 1999).

Soil Sterilization Both physical and chemical sterilization approaches now are available. Instead of using methyl bromide, many alternatives are being developed for soilborne pathogen control in commercial production. Solar sterilization, an environmentally friendly method, is increasingly used for the control of many soilborne diseases, although its influence on autotoxin degradation is unknown. However, soil sterilization can kill both pathogens and beneficial microbes in the soils. Interestingly, the sensitivity of soil microbes to chemicals sterilizers such as calcium cyanamide varies with their species and many microbes recovery faster than pathogens (Shi et al., 2009).

Introduction of Beneficial Microbes Biotic factors play an important role in autotoxicity and pathogenesis. Beneficial microbes can be used to degrade phytotoxins, both autotoxins and microbial toxins (Caspersen et al., 2000; Asao et al., 2003, 2004b; Chen et al., 2011a). Microbes also can be developed for biological control. Many beneficial microbes with fungicidal capacity have been identified from suppressive soil and other soil types (Berg, 2009). Similarly, many isolates from suppressive soils or others can degrade autotoxins in the rhizosphere of continuously cropped plants (Asao et al., 2004b; Chen et al., 2011a). We found that inoculation with *Fusarium flocciferum* and *Cephalosporium acremonium* alleviated the autotoxicity induced by phenolic acids in cucumber (Yu,unpublished data). These beneficial microbes can be used alone or in combination with bioorganic fertilizers.

Physical Removal of Phytotoxins Activated charcoal has a strong capacity for adsorbing organic chemicals and is an ideal adsorbent for practical applications. In cucumber, tomato, and asparagus, a 15–30 % increase in productivity has been observed after using activated charcoal (Yu et al., 1993; Yu and Matsui, 1994; Asao et al., 2003). In addition, by applying TiO_2 photocatalysis and electro-degradation in a recycling hydroponic cultivation system, autotoxicity was avoided in asparagus and strawberry (Sunada et al., 2008; Miyama et al., 2009; Asaduzzaman et al., 2012).

Challenges and Outlook

As discussed above, intensive agriculture is prevalent in many countries and regions due to increased food and environmental concerns. This intensive approach may lead to soil sickness in croplands. Soil sickness is a complicated phenomenon, and the detailed mechanisms involved are not fully understood. In general, autotoxicity, disturbed microbial communities, and others are responsible for the observed phenomenon. The interaction between allelochemicals, autotoxins, and microbes is important. Additionally, it seems likely that causes may differ from plant to plant.

There is an increasing interest in the autotoxicity of crops, and more than 50 crops have been shown to have autotoxic potential. GS-MS and HPLC-MS have been the most popular instruments for the identification of autotoxins. However, sample preparation for the identification of soil autotoxins must be conducted carefully because contamination or artifacts from the culture or solvents, such as additives. In addition, the autotoxic potential of many crops has been established based only on the correlation of phytotoxicity and the dose of extracts in plant tissues, without evidence for autotoxins in the rhizosphere. Until now, not enough studies have followed a criterion similar to Koch's postulates, and furthermore, genetic evidence for the involvement of autotoxicity in soil sickness. Recently, Xu et al. (2012; see also Kato-Noguchi and Peters, 2013) demonstrated the allelopathic potential of rice plants by using knockouts of the relevant genes involved in the biosynthesis of momilactones. A detailed analysis of the genotypic differences in autotoxin metabolism, exudation and associated changes in knockouts plants and plant growth will enable us to provide important evidence for autotoxicity in these crops.

Soil is a complex matrix and many autotoxins can be easily modified by soil microbial communities (Kaur et al., 2009). To date, only a few of studies have investigated the behavior of autotoxins in soils during monocropping. Special attention should be paid when differentiating the active autotoxins from their inactive conjugates in the soils. In most cases, the concentrations of so-called autotoxins in soils are lower than that at the phytotoxic dose, and these autotoxins also are easily degraded by microbes. It is, therefore, difficult to explain why a 2–7 rotation or fallow period is necessary for these crops based on the fate of autotoxins. We need to find other important autotoxin candidates and study both the additive and synergistic effects of different autotoxins in the soil matrix. In addition, there are suppressive and conducive soils in agroecosystems, but the underlying mechanisms are largely unknown. It is unclear whether beneficial microbes can induce ISR in plants grown in suppressive soils. It will be interesting to compare the microbial communities and the behaviors of autotoxins in these soils.

The rhizosphere is a place with intensive interactions between root exudates, allelochemicals, and microbes, leading to beneficial and detrimental impacts on plant growth and disease prevalence in the plant-soil feedbacks. Allelochemicals or autotoxins in the rhizosphere directly or indirectly affect soilborne pathogens or other detrimental microbes. Root exudates of many plants also contain antimicrobial compounds; however, research in this area has been minimal. Biodiversity conservation with different cropping systems will be an increasingly important approach for the sustainable development of agriculture production and pest control. It is important to reexamine the usefulness of traditional agricultural management methods, and this is especially important in developing countries.

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