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Review Article

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Genetic Soil Disinfestation, A Conceptual Framework to Reduce Inoculum Potential of Soilborne Plant Pathogens

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Abstract

Soilborne pathogens are major constraints to the production of many food and non-food crops worldwide. A wide array of strategies are employed to reduce the activities of soilborne pathogens including chemical and non-chemical methods such as solarization, fumigation, anaerobic soil disinfestation, and soil chemical treatment. This article succinctly describes these methods and proposes the concept of "genetic soil disinfestation" as an additional innovative approach for managing soilborne pathogens. Although many components of "genetic soil disinfestation" include well known and familiar tools such as crop rotation, the concept of "genetic soil disinfestation" redefines cropping systems in a unified perspective with focus on using a genetic approach to optimize the attributes of hosts and nonhosts that significantly reduce the populations of soilborne plant pathogens and the efficiency of invasiness of these pathogens.

Keywords: Soil disinfestation, host resistance, nonhost resistance, genetic soil disinfestation, soilborne, inoculum potential

Introduction

The inoculum potential of plant pathogens embodies their intrinsic characteristics to survive, reproduce, spread, and initiate infection of their hosts. Preservation of inoculum potential is critical to the continuity of the life cycle of plant pathogens, and thereby constitutes a lurking threat to crop production systems. Reducing inoculum potential is central to management of plant pathogens in order to minimize the negative impacts of these pathogens on crop health.

An important tool used for reducing the inoculum potential of soilborne pathogens is soil disinfestation, which is achieved through a wide array of methods including fumigation, solarization, chemical treatment, and anaerobic soil disinfestation (Figure 1).

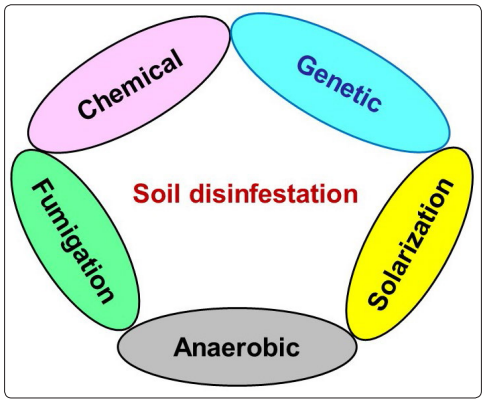

Figure 1: Generalized categories of soil disinfestation techniques including the proposed "genetic soil disinfestation."

The mechanisms of action, advantages, and disadvantages of each method are summarized in Table 1. Fumigation achieves soil disinfestation through the application of formulations with properties to emit toxic volatiles once applied to soil. Examples include chemical fumigants such as chloropicrin, metam sodium, metam potassium, and 1,3-dichloropropene. Other formulations include residues of bioactive crops such as brassicaceous crops, which contain high levels of glucosinolates whose degradation products have been shown to be lethal to pathogens and pests such as weeds [1,2]. Additionally, biofumigation may be accomplished through the use of microbial formulations demonstrated to emit volatiles that interfere with the phenology of pathogens [3].

Solarization encompasses the entrapment of solar heat in soil to accomplish reduction of pathogenic populations in soil [4]. Solar heating of soil is attained through utilization of plastic cover sheets or plastic mulching. Adequate soil moisture content is critical in optimizing the thermal properties of the soil to build lethal heat level. Solarization not only thermally affects the population of plant pathogens, it can also enhance the activities of antagonistic microorganisms [5].

In anaerobic soil disinfestation, also known as reductive soil disinfestation or biological soil disinfestation [6], the soil is amended with a carbon source, irrigated to field capacity, and tarped with an impermeable plastic film. During this process, anaerobic conditions are established in the soil, volatile organic compounds are released in the soil, and microbial activities are also increased in the soil. Collectively, all these changes enable the suppression of soilborne pathogens [6].

All of these methods may be used singly or in combination. Butler et al. used soil solarization in conjunction with anaerobic soil disinfestation to reduce populations of soilborne pathogens in vegetable grown in raised beds [7]. Solarization can be used in combination with biofumigation or other organic amendments in a process known as biosolarization to disinfest soil [8]. Yücel et al. showed that combining solarization and metam potassium yielded a greater reduction of the severity of Fusarium wilt, Rhizoctonia root rot, and root knot nematode infection in greenhouse tomato than when solarization and metam potassium were used alone [9].

Table 1: Mechanisms, advantages, and disadvantages of generalized categories of soil disinfestation

Soil disinfestation	Mechanisms	Advantages	Disadvantages
Solarization	Heating	*Broad range, non-selective action *Increase in antagonistic populations	* Long time periods required for heat to build to an effective threshold *Dependent on soil moisture content
Fumigation	Toxic volatiles	*Broad range, non-selective action	*Gas movement and distribution in soil could be hampered by soil conditions and application methods *Can reduce the populations of antagonists to the advantage of target pathogens
Chemical	Chemical toxicity	*Selective and non-selective depending on whether chemicals are pathogen-specific or are broad range	*Can reduce populations of antagonists *Risk of pathogenic resistance
Anaerobic (Biological or Reductive)	Anaerobic conditions	*Broad range, affecting high-oxygen microorganisms	*Efficacy dependent on carbon source, tarping materials, and temperature (low temperature may limit efficacy)
Genetic	Host and nonhost resistance	*Exploits host-pathogen and nonhost-pathogen interactions	*May be long-term process *May increase selection pressure of pathogens in hosts or increase adaptation in nonhosts

In this work, a new perspective on soil disinfestation is proposed under the term of "genetic soil disinfestation," which distinguishingly uses a genetic approach that exploits the attributes of host resistance (sensu stricto) and nonhost resistance (sensu lato) to reduce inoculum potential in soil (Table 2). The distinction between host and nonhost is defined using the terms of "symptomatic host" and "asymptomatic host," respectively, as proposed by Malcolm et al. based on tissue colonization [10]. Further, the categorization of the term "nonhost" into Type I and Type II by Mysore and Ryu is used and explained below [11]. The extent of parasitic and saprophytic colonization of host and nonhost tissues by soilborne pathogens is hypothesized as the most critical determinant of inoculum potential in soil. The proposed new concept of genetic soil disinfestation delineates a pedestal for research directed at identifying and exploiting host resistance and nonhost resistance to reduce inoculum potential in soil and plant invasion through optimization of host-pathogen and nonhost-pathogen interactions. Host genotypes and nonhost genotypes with high capacity to resist pathogenic invasion and colonization are planted during multiple cropping cycles prior to planting highly desirable susceptible host genotypes.

Components of Genetic Soil Disinfestation

Host Resistance

Genetic soil disinfestation, sensu stricto, is the use of host-specific resistance to reduce the inoculum potential in soil. The basic tenet of host resistance lies in the selective inclusion and exclusion of host-adapted pathogens from partaking in the infection of the host. Utilization of host resistance may efficiently suppress the inoculum potential of selected pathogenic strains whereas other strains remain unaffected. The feasibility of this approach is supported by numerous examples in the literature, few of which are discussed below.

In the pathosystem of *Fusarium oxysporum* f. sp. *vasinfectum*-cotton (*Gossypium* sp.), Wang et al. compared disease severity in cotton planted in soil previously cropped to the most susceptible cultivar Siokra 1-4, moderately susceptible cultivar Siokra L22, less susceptible cultivar DP90, maize (*Zea mays*), sorghum (*Sorghum bicolor*), and soybean (*Glycine max*) [12]. Disease severity of Fusarium wilt was significantly reduced in the most susceptible cotton cultivar Siokra 1-4 when it was planted in soil cropped previously with the less susceptible cultivar DP90 compared to when it was planted in soil cropped previously with Siokra 1-4, with the moderately susceptible cultivar Siokra L22, and other crops. Similar results were reported by Katan et al. who showed that disease incidence of Fusarium wilt in a susceptible Pima cotton cultivar following cropping with the same cultivar was 41% whereas disease incidence was 4% when the susceptible cultivar was planted after cropping with a resistant Acala cotton cultivar [4].

Working on brown stem rot (BSR) disease of soybean (*Glycine max*), caused by *Phialophora gregata* f. sp. *sojae*, Tachibana et al. showed that continuous cropping of BSR- resistant cultivars resulted in the reduction of the disease in subsequent susceptible cultivars [13]. Disease incidence in BSR-resistant cultivars was approximately 40 and 82% when these cultivars were planted in soil that has been continuously cropped for 4 years with the BSR-resistant genotype A3 and the BSR-susceptible cultivar Coles, respectively. In contrast, disease incidence in BSR-susceptible cultivars was approximately 70 and 97% when these cultivars were planted in soil that has been continuously cropped for 4 years with the BSR-resistant genotype A3 and the BSR-susceptible cultivar Coles, respectively. Such decrease in disease level was postulated to be due to a decrease in pathogen inoculum in soil. However, in a later study by Hughes et al., it was indicated that the decrease in disease level under continuous cropping of BSR-resistant soybean was probably due to the increase in populations of the less aggressive genotype B of *P. gregata* f. sp. *sojae* [14].

Hwang et al. compared the effect of three cropping cycles of resistant and susceptible cultivars of canola (*Brassica napus*) and of three

cycles of fallow on the resting spore populations of *Plasmodiophora brassicae* (causal agent of clubroot) [15]. There were no differences between three cropping sequences of the resistant cultivar 45H29 and three cycles of fallow with regard to the resting spore populations. However, continuous cropping of the resistant cultivar and continuous fallow significantly reduced the populations of resting spores compared to continuous cropping of the susceptible cultivar. Additionally, the severity of clubroot was significantly reduced in the susceptible canola cultivar planted after three cycles of cropping with the resistant cultivar or three cycles of fallow, compared to when the susceptible canola cultivar was planted after three cropping cycles with the susceptible cultivator. In this study, it was indicated that the resistant cultivar neither increased the inoculum level nor increased the germination of spores in soil.

In greenhouse and field studies comparing root colonization of broadleaf tobacco (*Nicotiana tabacum*) by the wilt-causing fungal pathogen *F. oxysporum* f. sp. *nicotianae* (FON), LaMondia reported that the number of colonies of FON per length of root (in centimeter) was greater in wilt-susceptible tobacco genotype 86-4 than in wilt-resistant tobacco genotypes C8 and C9 [16]. Additionally, final soil populations of FON were lower in soil planted with the wilt-resistant genotypes than in soil cropped to the wilt-susceptible cultivar.

Nonhost Resistance

Genetic soil disinfestation, sensu lato, focuses on reducing inoculum potential in soil using nonhost resistance, which embodies reaction to non-adapted pathogens ranging from immunity (no colonization) to some degree of colonization (Table 2).

Table 2: Hypothesized effects of host and nonhost characteristics on inoculum potential at various levels of colonization (parasitism and saprophytism)

Host/nonhost characteristics[a]	Colonization[b]		
	Parasitism	Saprophytism	
		Low	High
Host-specific resistance (Symptomatic host)			
Immune	None	L	H
Resistant	Low	L	H
Susceptible	High	H	H
Nonhost resistance (Asymptomatic host)			
Type I/Immune	None	L	H
Type II/Not immune	Low	H	H

[a] The distinction between host and nonhost is delineated using the terms of "symptomatic host" and "asymptomatic host," respectively, as proposed by Malcolm et al. [10]. Type I and Type II nonhost terms are as defined by Mysore and Ryu [11] in the text.

[b] The combined effects of parasitism and saprophytism may result in low (L) or high (H) inoculum potential level. In the case of immunity, the pathogen is unable to colonize neither the specific host and the nonhost displaying type I nonhost resistance (parasitism = none). All other cases result in low or high parasitism. The level of saprophytism may be low due to several factors including high level of antagonism, or may be high due to, among other plausible reasons, low level of antagonism.

Mysore and Ryu described a model comprised of two types of nonhost resistance, type I and type II [11]. In the type I nonhost resistance, no symptoms are caused in the nonhost plants because the plants are able to build a multi-faceted defense system that keeps the pathogens at bay. This defense system includes structural and biochemical changes such as formation of physical barriers (strengthening of cell walls and formation of papillae) production of secondary metabolites such as phytoalexins. Systemic acquired resistance (SAR), which embodies the expression of pathogenesis-related (PR) genes, is activated. Consequently, colonization of nonhost plants may be nil or limited.

In the type II nonhost resistance, visible symptoms are developed as a result of hypersensitive reaction (HR). Additionally, SAR is activated during this type II nonhost resistance. Type II nonhost resistance implies a breach of the nonhost defense system and underscores the possibility of colonization of the nonhost plants at varying degree. Colonization of nonhost plants paves the way for possible production of pathogenic inoculum, and thereby constitutes a risk for perpetuating the pathogens in production systems.

Crop rotation, practiced through the cultivation of nonhost crops, has been employed through ages to avert the damaging effects of pathogens and pests. For example, in the pathosystem of sugar beet (*Beta vulgaris* subsp. *vulgaris*)-*Rhizoctonia solani*, cropping with the nonhost wheat (*Triticum aestivum*) for two years prior to planting the host sugar beet significantly reduced inoculum potential of *R. solani* in soil [17].

Chen at al. showed that rotating Chinese cabbage (*Brassica rapa* subsp. *pekinensis*) with nonhost potato onion (*Allium cepa* var. *aggregatum*) decreased the incidence of clubroot disease, caused by *Plasmodiophora brassicae*, compared to a monoculture of Chinese cabbage [18]. Additionally, the incidence of clubroot disease decreased by 40% in Chinese cabbage planted in soil treated with root exudates from potato onion.

Efficiency of Host and Nonhost Resistance

A point of interest is the relative efficiency of host resistance and nonhost resistance. Host resistance has been shown to have higher efficiency in soil disinfestation than nonhost resistance. Severity

of Fusarium wilt (*Fusarium oxysporum* f. sp. *vasinfectum*) was significantly reduced in the most susceptible cotton cultivar Siokra 1-4 when it was planted in soil cropped previously with the less susceptible cultivar DP90 compared to when it was planted in soil cropped previously with maize (*Zea maydis*), sorghum (*Sorghum bicolor*), or soybean (*Glycine max*) [12].

Moussart et al. examined under greenhouse conditions the dynamics of the inoculum potential of *Aphanomyces euteiches* in soil cropped to perennial rye (*Lolium perenne*), which is a nonhost to the pathogen, and in soil cropped to several host legume species and cultivars including pea (*Pisum sativum*), lentil (*Lens culinaris*), alfalfa (*Medicago sativa*), faba bean (*Vicia faba*), common vetch (*Vicia sativa*), clover (*Trifolium pratense*), and lupin (*Lupinus alba*) [19]. Among these leguminous hosts, clover, lupin, and a cultivar of vetch were reported as resistant to *A. euteiches* whereas pea, lentil, alfalfa, and a cultivar of vetch were reported as susceptible to *A. euteiches*. Following 10 cycles of monoculture, the inoculum potential of *A. euteiches* in soil was increased under the continuous cropping of susceptible crop cultivars whereas the inoculum potential decreased or remained unaffected in soil with monoculture of resistant cultivars, or under monoculture of the nonhost perennial rye, or when soil was not planted with any crops.

Efficiency of nonhost crop rotation in reducing the populations of pathogens in soil is not consistent in the literature [20]. Several factors underpin this inconsistency including genetic structure of the pathogenic populations, nature of rotational crops, length of rotation, and asymptomatic infection of rotational crops [20,21]. However, for each pathosystem, effort needs to be focused on identifying genotypes of nonhost crops that affect significantly the inoculum potential in soil.

Mechanisms of Genetic Soil Disinfestation

The reduction of soil inoculum associated with cropping of resistant crop cultivars and nonhost crops may be due, among other mechanisms, to changes in the biochemical properties of the rhizosphere soil and bulk soil owing to root exudation and secondary metabolites [18,22]. These changes may affect directly all aspects of the phenology of soilborne pathogens including spore production, survival, and germination. For example, germination of microsclerotia of *Cylindrocladium crotalariae* was significantly reduced in exudates of resistant genotypes of peanut than in exudates of the susceptible genotypes [23].

Additionally, biochemical changes may affect soil microbiome leading to the recruiting and building up of microbiome that is antagonistic to the pathogens [22]. Extensive research on rhizosphere of resistant and susceptible genotypes has demonstrated differences in microbiome diversity and abundance under resistant genotypes than under susceptible genotypes. It was reported that resistant genotypes produced higher level of carbon, which may have contributed to enhanced activity of antagonistic microorganisms and thereby to the decrease in germination of microsclerotia of *Cylindrocladium crotalariae* [23]. Mendes et al. found that the abundance of beneficial bacterial communities in the rhizosphere of common bean (*Phaseolus vulgaris*) was positively correlated with resistance to the root pathogen *Fusarium oxysporum* [24]. Additionally, functional traits associated with antifungal compounds were more abundant in the beneficial bacterial communities in the rhizosphere of the resistant common bean cultivar than in the rhizosphere of the susceptible common bean cultivar.

Quantification of Genetic Soil Disinfestation

Genetic soil disinfestation may be assessed through quantification of soil inoculum, plant tissue colonization or invasiness, and disease incidence and severity [25-27]. Quantification of soil inoculum may be performed through semi-selective growth media for culturable microorganisms or through PCR-based methods [17]. Additionally, soil inoculum may be quantified through bioassays with whole indicator plants or tissue pieces of indicator plants [17,28]. Plant tissue colonization may be evaluated through the frequency of isolation of target pathogens from roots and stems and colony-forming units (CFU) from root and stem tissues [16,25,26,29]. The frequency of root colonization is assessed in a two-step process including surface sterilization, sectioning into small segments, and plating these segments on general growth media or semi-selective growth media. The percentage of root segments yielding the target microorganism is used as the frequency of isolation of that particular microorganism. In lieu of plating, root segments may be milled into a powder from which a suspension is prepared and serially diluted and plated on semi-selective growth media to estimate the number of CFU. Both plating of root segments and determination of CFU are tedious and time-consuming. Alternatively, PCR-based techniques may be used to estimate the extent of colonization in root [17]. Based on the various variables measured, an index of genetic soil disinfestation may be derived to assess the relative efficiency of host resistance and nonhost resistance in reducing soil inoculum potential.

Limitations and Assumptions of Genetic Soil Disinfestation

Limitations of Host Resistance

There is a concern that continuous cropping of resistant host genotypes may exert a selection pressure leading to the increase of various genotypes of pathogenic strains. However, this concern may be addressed by routine monitoring of populations of pathogens in order to gauge changes in these pathogenic populations.

Another concern consists of resistant host genotypes serving as bait plants, that is, enabling the perpetuation of pathogens within the tissue of resistant genotypes. Residues from such genotypes could replenish soil inoculum reservoir upon incorporation and degradation in soil. The extent of root colonization of resistant genotypes should be assessed along the capacity of the resistant genotypes in reducing soil inoculum.

Limitations of Nonhost Resistance

Conceptually, type I nonhost resistance is desirable because it counters the phenology and activities of non-adapted pathogens [11]. This may be tenable for as long as the same nonhost crops are not continuously planted. Continuous cropping of nonhost crops may lead to adaptation of pathogens to the nonhost crops. This adaptation may manifest under several scenarios such as establishment of asymptomatic infections [20,21].

Of major concern is the amount of inoculum produced by non-adapted pathogens on the nonhost crops during rotational periods [20]. Additional concern is the pathogenicity of isolates from nonhost crops on host crops. For example, many weed species are known to harbor various soilborne pathogens. Isolates of many pathogens such as *Verticillium dahliae* recovered from asymptomatic weeds

have been demonstrated to cause typical disease symptoms when inoculated into the host crops [30,31]. It was postulated that weeds, as symptomless carriers, may serve as major contributors to the persistence of *V. dahliae* under field conditions if not managed adequately [31]. Even in scenarios of diversified nonhost cropping systems, adaptation to some crops in such systems may be observed. In light of these scenarios, the use of nonhost resistance to reduce inoculum potential may be practical if pathogen adaptation is minimum.

Assumptions in Genetic Soil Disinfestations

The proposition for using a genetic approach to soil disinfestation as presented in this work assumes that the genetic characteristics of hosts and nonhosts are the primary driving forces in crop production. However, Production environment may influence the outcome of the interactions among hosts, nonhosts, and soilborne pathogens. Screening and selection of hosts and nonhosts with high capacity for genetic soil disinfestations will need to take into account the stability of the response of these hosts and nonhosts to production environment variables including inputs such as irrigation, fertilizers, and pesticides, and extremes in edaphic variables such as moisture (drought and flooding).

Summary and Perspective

The concept of genetic soil disinfestation redefines cropping systems with focus on using a genetic approach to optimize the attributes of hosts and nonhosts that significantly reduce the populations of soilborne plant pathogens and the efficiency of invasiness of these pathogens. Hosts and nonhosts with high capacity for genetic soil disinfestation should, among other things, resist invasion or colonization and saprophytic growth of pathogens. These attributes are quantifiable and can be used to carry out a benchmark evaluation of hosts and nonhosts for their efficiency in reducing the inoculum potential of soilborne pathogens.

The implementation of the concept of genetic soil disinfestation does not necessitate any drastic changes in cropping systems. It will require a systematic planning of existing crop management schemes to include hosts and nonhosts based on their capacity in reducing inoculum potential. In order to assist agricultural practitioners in this endeavor, the research community must deploy effort in establishing parameters that are reliable and easy to measure for gauging the genetic capacity of candidate hosts and nonhosts for soil disinfestation. In all, the concept of genetic soil disinfestation provides a new unified framework for managing the inoculum potential of soilborne pathogens and opens a new direction of research to validate the concept and broadness of its applicability.

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