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Review

Q:1

Biofumigation: Opportunities and Challenges for Control of Soilborne Diseases in Nursery Production

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Abstract

Soilborne diseases reduce crop performance, increase costs to the nursery producers, and can cause potential ecological damage to the natural environment. In particular, soilborne diseases caused by *Phytophthora nicotianae* and *Rhizoctonia solani* are the most economically important problems of southeastern U.S. nursery producers. Methyl bromide was widely used as a standard treatment in many parts of the world until the implementation of the Montreal Protocol. Since then, many chemical and nonchemical soilborne disease management methods have been tested but are not yet providing effective and consistent results like methyl bromide. Cover crops that belong to the Brassicaceae family can be incorporated into the soil to control soilborne diseases, and this process is widely known as biofumigation. Glucosinolates that are available inside Brassicaceae plant cells can be hydrolyzed into isothiocyanates, and these compounds are proven to be highly biocidal to many microorganisms (including fungi, oomycetes, nematodes, and bacteria), insects, and germinating weed seeds. The use of biofumigant cover crops is a newer area of research in woody ornamental nursery production that has been previously explored most extensively in row crop, vegetable, fruit, and flower production. This review article compiles previous research observations in biofumigation while emphasizing the potential of biofumigation to control diseases in nursery production caused by soilborne pathogens.

Q:2

Nursery Production

Woody ornamental plants are produced by the nursery industry primarily for aesthetic value and are marketed for retail consumption by homeowners and landscaping professionals. Additionally, specialty nurseries cater to smaller industries, such as orchards, lumber, and hazard (i.e., storm water or wind) mitigation (Rosen 1990). In the 1970s, Baker and Linderman (1979) found 1,100 genera of plants were grown for the global ornamental plant industry, and the staff of the L. H. Bailey Hortorium (1977) compiled a list of cultivated ornamental plants in North America totaling more than 20,000 species. Although the exact number of species in current production is not available, for the last decade there have been more than 1,000 plant patent applications each year in the United States, almost triple the number occurring annually in the 1980s and 1990s (U.S. Patent and Trademark Office 2016). In 2014, there were 8,200+ nursery producers in the United States, and nursery crop sales comprised 31% of all horticultural sales, exceeding $5.1 billion (USDA 2016). California ($958.5 million), Florida ($574.7 million), and Oregon ($469.6 million) were the leading nursery producing states, and the largest number of horticultural producers (5,000+) were located in the southeastern United States (USDA 2016).

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Nursery producers are vulnerable to losses owing to root and crown rot diseases caused by soilborne pathogens and, in 2015, these losses were estimated to be approximately 5% of the farm gate value for field and container nursery production (Little 2015). Leading southeastern U.S. nursery producers and university representatives rate root and crown rots resulting from pathogens such as *Phytophthora* spp. and *Rhizoctonia solani* as their most important concern in nursery production (IPM 2009). Additionally, the premium placed on aesthetically perfect ornamental crop specimens as well as the intensive nature of woody ornamental production has resulted in a modern nursery industry that is heavily reliant on synthetic, broad-spectrum pesticides to control insects and diseases. Development and implementation of alternative, sustainable biofumigant cover crop protocols should improve nursery production while simultaneously reducing the amount of pesticides introduced into the environment.

Important Soilborne Pathogens in Southeastern U.S. Nursery Production

***Phytophthora nicotianae*.** *P. nicotianae* Breda de Haan (domain, Eukaryota; superphylum, Heterokonta; class, Oomycetes; order, Pythiales; family, Pythiaceae; and genus, *Phytophthora*) can infect 255 genera in 90 families (Cline et al. 2008), accounts for billions of dollars in crop losses annually worldwide (Kamoun et al. 2014; Wawra et al. 2012), and is a leading cause of losses in commercial nursery production (Blair et al. 2008; Erwin and Ribeiro 1996). Although it was likely introduced multiple times prior through trade, *P. nicotianae* was first recorded in the United States in southern Georgia in 1915 (Lucas 1958).

P. nicotianae has been identified as one of the most common pathogens affecting ornamental plants (Moralejo et al. 2009; Pane et al. 2005). The continuous and repeated growth of different types of host plants in the same soil or propagation beds by woody ornamental nurseries allows *P. nicotianae* to complete several disease cycles per year (Hu et al. 2008). The extensive spread of this pathogen is partially owing to the large number of zoospores produced per sporangium, and its persistence can be attributed to its ability to produce oospores and chlamydospores to overwinter or endure during unfavorable conditions in the rhizosphere of host plants (Erwin and Ribeiro 1996). Zoospores have two types of flagella (anterior and posterior) in two different sizes to assist them in swimming, and chlamydospores can be dispersed by irrigation water, rain splash, and soil movement (Thomson and Allen 1974). As a result, the pathogen thrives in wet or moist conditions and can spread quickly as zoospores and sporangia swim through irrigation reservoirs, irrigation drainage water, streams, or rivers (Ghimire et al. 2011). Repeated cropping at the same field, dense nursery crop planting, and the use of recycled irrigation water in nursery operations further facilitate *Phytophthora* infection (Ribeiro and Linderman 1991).

Common symptoms include wilting and chlorosis of leaves and stem, crown, and root rot. The most characteristic symptoms of *Phytophthora,* a blackened lower stalk and random disking of the pith, can present on both above- and below-ground plant parts (Shew 1987).

Rhizoctonia solani. *R. solani* Kühn (kingdom, Fungi; division, Basidiomycota; class, Agaricomycetes; order, Cantharellales; family, Ceratobasidiaceae; and genus, *Rhizoctonia*) is a ubiquitous soilborne pathogen that may attack host plants at any life stage to cause damping-off (in both pre- and postemergence phase), root and stem rot, leaf spot, leaf blight, and foliar web blight (Hyakumachi et al. 2005; Rinehart et al. 2007). It can also exist as a saprophyte (Menzies 1970). *Rhizoctonia* spp. affect more than 500 plant species (Farr et al. 1995) including ornamental nursery crops, agronomic crops (species in the Solanaceae, Poaceae, Fabaceae, Asteraceae, and Brassicaceae families), fruit and forest trees, and turfgrasses (Couch 1995; Ogoshi 1987; Sneh et al. 1991; Verma 1996). First described by Julius Kühn in 1858 (Kühn 1858), *R. solani* is the most widely known and studied of the genus *Rhizoctonia.*

R. solani reproduces asexually through hyphae (vegetative mycelium) and sexually by the formation of basidiospores (Flentje et al. 1970), although sexual reproduction is rare. Sclerotia, the resting stage of *R. solani,* are critical to survival during winter and other unfavorable conditions. Sclerotia may survive in the soil for many years (Baker 1970; Echandi 1965). A 2-year field study on *R. solani* ecology and epidemiology concluded almost all pathogen activity was confined to the 0- to 5-cm upper soil (Papavizas et al. 1975), because it is attracted to plant secretions in the rhizosphere. When the supply of nutrients from decaying plant debris becomes insufficient or unavailable, the virulence of the pathogen is decreased (Doornik 1980). However, *R. solani* is an efficient competitor when other resources are limited, because it can exploit carbon sources seldom used by other microorganisms, such as cellulose (Deacon 1996). Infection is initiated when a germinating sclerotium produces mycelia or hyphae toward a host plant that is exuding sugars, amino acids, organic acids, and phenols into its rhizosphere (Keijer 1996).

Brassicaceae Cover Crops

Cover crops are primarily used in agriculture to improve the growth of cash crops while minimizing financial and environmental costs of synthetic inputs. Cover crops are critical for reducing erosion resulting from soil exposure, controlling soilborne pathogens by acting as a break crop (intercropping or rotation crop), increasing cash crop yield by improving soil health (green manures), and inhibiting weed growth through competition (Bowman et al. 1998). In 2008, nearly 36,000 acres of land was used for "green manure" cover crop production in the United States, and acreage devoted to cover crop production increased 15% annually from 2002 to 2008 (Economic Research Service 2010).

The Brassicaceae family is a monophyletic plant group of about 338 genera and 3,709 species distributed worldwide and includes turnip (*Brassica rapa* L.), rapeseed (*B. napus* L.), mustards (*Sinapis* spp.), and radish (*Raphanus sativus* L.), which can be used as cover crops (Clark 2007). The most economically important genus is *Brassica*, which contains 37 species and is commonly cropped for edible roots, seeds, leaves, stems, buds, and flowers (Gomez-Campo 1980). Beyond the established benefits of soil conservation and improvement, *Brassica* cover crops can also control soilborne pathogens (Ngouajio and Mutch 2004).

Biofumigation

Before 2005, soil fumigation with methyl bromide was the primary and highly effective method of controlling soilborne diseases. Unfortunately, methyl bromide is also a potent greenhouse gas, and its complete phase-out was mandated by the Montreal Protocol in 1987.

First coined by J. A. Kirkegaard and his associates in 1993, the term "biofumigation" refers to an alternative control method that utilizes naturally occurring biocidal compounds, specifically isothiocyanate compounds (ITCs), produced through the hydrolysis of glucosinolate compounds (GSLs) containing plants (Kirkegaard et al. 1993, 1998, 1999; Matthiessen and Shackleton 2005), to suppress pathogenic soil microorganisms such as fungi, bacteria, and nematodes (Angus et al. 1994; Brown and Morra 1997). Kirkegaard's biofumigation process consisted of growing GSL-containing Brassicaceae plants as cover crops and then macerating and incorporating the foliage into the soil to facilitate the release of ITCs (Kirkegaard et al. 1993). ITCs positively affect rhizosphere community composition, suppressing soilborne plant diseases while having limited effect on common beneficial microbial species, such as *Trichoderma* (Galletti et al. 2008). Incorporated cover crops can also stimulate beneficial microbial populations by increasing the amount of carbon substrate, allowing them to compete with the reduced numbers of pathogenic microbes for resources in the soil, and can help maintain lower disease levels (Griffiths et al. 2011). Subsequent research using oriental mustard, oilseed radish, and yellow mustard cover crops also demonstrated plant pathogen population reduction in the soil (Sarwar et al. 1998). Experimental results of Brassicaceae cover crops in controlling soilborne pathogens are listed in Table 1. To maximize the benefits of biofumigation, however, these processes need to be compatible with the existing farming system. Farms already using green manure can readily adjust to this technique by replacing current cover crops with a biofumigant cover crop (Matthiessen and Kirkegaard 2006).

GSLs. Plants and seed meals containing GSLs have a long history of use as rotation/break crops, green manures, or soil amendments owing to their biocidal properties (Brown and Morra 1997). Most studies have been concerned with GSL-related suppression, and experimental results demonstrated significant control of soilborne pathogens and weed seed germination (Matthiessen and Kirkegaard 2006). Almost all species of Brassicaceae contain some GSLs (Kjaer 1976).

GSLs are β-thioglucoside N-hydroxysulfates containing a side (R) group (Fahey et al. 2001) and are classified into three groups based on their amino acid precursors: (i) aliphatic, derived from alanine, methionine, valine, leucine, and isoleucine; (ii) aromatic,

TABLE 1
***Brassica* cover crops with effectiveness against soilborne pathogens in trials**

Pathogen	Cover crop	Suppression (%)	Reference
Aphanomyces euteiches	*Sinapis alba*	32	Muehlchen et al. (1990)
Pyrenochaeta lycopersici	*Brassica rapa*	12–52	Amenduni et al. (2004)
	B. oleracea	23–43	
Pythium spp.	*B. napus*	0	Stephens et al. (1999)
	B. juncea	0	
Ralstonia solanacearum	*B. juncea*	62	Akiew and Trevorrow (1999)
Rhizoctonia solani	*B. juncea*	25	Van Os et al. (2004)
Sclerotinia minor	*B. juncea*	68	Daugovish et al. (2004)
	S. alba	91	
Q:8 *Streptomyces scabies*	*B. oleracea*	90	Gouws and Wehner (2004)
Verticillium dahliae	*B. oleracea*	35	Subbarao and Hubbard (1996)

derived from tyrosine and phenylalanine; and (iii) indole, derived from tryptophan (Fenwick et al. 1983). Toxicity and range of activity of ITCs derived from GSLs are R group dependent. Aliphatic GSLs are more volatile than aromatic GSLs, and increased volatility is associated with increased pathogen toxicity of the ITCs (Lewis and Papavizas 1970). GSL compounds exist separately in plant cells from the enzyme myrosinase (Manici et al. 1997).

Myrosinase. Myrosinase is a cytosolic enzyme present in cell membranes surrounding a vacuole containing GSLs (Lüthy and Matile 1984). Individually, GSLs and myrosinase demonstrate minimal biological activity (Manici et al. 1997). However, when plant cells are ruptured (Vig et al. 2009), myrosinase catalyzes the hydrolysis of the β-D-thioglucopyranoside bond in glucosinolates, resulting in a variety of products with different structures and properties (Bellostas et al. 2007).

Myrosinase cleaves the thioglucoside linkage to produce glucose compounds and unstable thiohydoxymate-*O*-sulfates (Bones and Rossiter 2006), which can spontaneously rearrange and form a variety of biologically active compounds such as ITCs, nitriles, elemental thiocyanates, sulfur, epithioalkanes, and oxazolidine-2-thiones (Grubb and Abel 2006; Holst and Williamson 2004). Compound production depends on several factors, including glucosinolate R-group, pH, the presence of myrosinase-interacting proteins and cofactors, and the concentration of ferrous ions (Grubb and Abel 2006). Myrosinase activity exhibits specificity to GSL compounds (Durham and Poulton 1990), although it is genetically similar to other β-glycosidases (Lenman et al. 1993) that do not.

ITCs. ITCs are chemicals that are functionally formed by replacing the oxygen in the isocyanate group with sulfur (Bedane Kibrom and Singh Girija 2015). They occur widely in nature but can also be manufactured synthetically in methyl ITC form. In Brassicaceae plants, tissue disruption causes myrosinase to catalyze a hydrolysis reaction that converts GSLs into aliphatic ITC and other hydrolyzed products like glucose, thiocyanates, nitriles, epithionitriles, oxazolidine-2-thiones, and hydroxynitriles (Gimsing and Kirkegaard 2009). Under field conditions, aliphatic ITC is more toxic to microorganisms than aromatic ITC (Matthiessen and Shackleton 2005), although the low volatility of aromatic ITC results in longer-term persistence in the soil (Kirkegaard and Sarwar 1998). ITCs can remain in the soil for a few days to a few weeks. Half-lives of methyl ITC in various soils stored inside gas-tight containers were 0.5 to 50 days at 15°C (Smelt et al. 1989). In rapeseed meal-amended soil, ITC levels decreased by 90% within 24 h (Brown et al. 1991). In contrast, methyl ITC levels only decreased by 34% over 10 h in a laboratory setting using spiked soil (Munnecke et al. 1962). These values illustrate more volatile loss for natural ITC compounds than synthetic, commercially produced compounds. Increasing organic matter results in increased soil sorption of methyl ITC (Smelt and Leistra 1974), so soils with a high percentage of organic matter will volatilize less methyl ITC than more mineral soils (Sirons 1973). In tests of soil texture, sandy loam soil (8% clay, 0.67% organic matter) experienced the greatest rate of loss, whereas the lowest volatilization was recorded by loam soil with more clay and organic matter (25% clay, 2.03% organic matter) (Munnecke and Martin 1964), illustrating the importance of soil composition on ITC. Temperature is also a critical factor, with higher temperatures correlating with higher amounts of vaporized ITC, resulting in a faster rate of dispersion from the soil (Borek et al. 1995). Because higher volatility is positively correlated with higher pathogen inhibition, higher temperatures have been shown to increase the effectiveness of ITC (Gamliel and Stapleton 1993). ITC volatility and soil moisture content are inversely correlated, so that wetter soils experienced increased ITC longevity in the soil. In the headspace of soils with lower water content, higher rates of methyl ITC disappearance were measured (Turner and Corden 1963).

Biofumigation Opportunities and Challenges in Nursery Production

Biofumigant cover crops have been heavily investigated for agricultural applications, but practical applications in the nursery industry are currently limited. A wide range of biofumigant cover crops are available, but efficacy is not well documented in research literature for nursery production; at the same time, agronomic factors (such as seed rate, time of sowing, and optimal incorporation time with/without solarization), environmental factors (soil temperature and moisture), and soil or growing medium factors (soil Q:5 type, organic matter, and fertilizer contents) provide new opportunities and challenges for testing and validation of biofumigant cover crops in nursery production.

Most of the studies conducted on GSL-related suppression show statistically significant ability to control soilborne pathogens and weed seed germination (Matthiessen and Kirkegaard 2006). However, some members of the Brassicaceae family are also susceptible to *R. solani* (Gupta 1985; Huber et al. 1992). *R. solani*-caused damping-off and root rot are important diseases of oilseed rape (*B. napus*) and rapeseed (*B. rapa*) in western Canada (Berkenkamp and Vaartnou 1972; Ellis 1983; Sippell et al. 1985). A preestablished population of *R. solani* may result in severe seedling diseases of oilseed rape, with establishment loss of 80 to 100% and final yield losses of up to 30% reported worldwide (Khangura et al. 1999; Tahvonen et al. 1984). It is therefore critical to develop a nursery management strategy that considers the resistance of a *Brassica* spp. to the pathogen in question prior to initiating a biofumigation protocol.

Nursery production systems are complicated to manage owing to the many species and genera that may be grown on a single farm in different platforms such as field and raised bed (with growing medium). The nature of this highly intensive production system combined with an almost unlimited number of varieties or cultivars of woody ornamentals and other factors contribute to soilborne diseases, specifically caused by *P. nicotianae* and *R. solani*, in southeastern U.S. nursery production. Advancing nursery production toward sustainability requires development and demonstration of environmentally friendly management strategies such as biofumigation, assessing the economics of new strategies to validate the costs and benefits of adoption, and then extension of the new methodologies to nursery producers. If biofumigation for *Phytophthora* and *Rhizoctonia* disease management is to be widely accepted, researchers must identify biofumigant cover crops compatible with standard woody ornamental field transplant and propagation practices and develop cost-effective processes and workflows that are robust across nursery crops for different production platforms. These are the next critical steps to improve the both the sustainability and profitability of woody ornamental production while simultaneously minimizing soilborne disease.

In conclusion, cover crops provide a wide range of benefits in production systems: they suppress weeds, reduce erosion, preserve soil quality, provide organic matter, and aid nutrient cycling (Mutch and Snapp 2003); biofumigation is a welcome addition. The best candidates for biofumigation implementation are farms already using a green manure system, because they can readily add a biofumigant cover crop into their cover crop rotation (Matthiessen and Kirkegaard 2006). Although there are challenges to using biofumigant cover crops, the benefits to soil health, nursery crop productivity, and the environment merit need further investigation and implementation for southeastern U.S. nursery production as well as other regions.

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