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Fusarium wilts of ornamental crops and their management

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ABSTRACT

The production of ornamental plants continues to be a thriving and expanding industry in the United States, Canada, South America, Australia, and Europe, supported by plant industries in many developing countries. Fusarium wilt diseases, however, continue to plague the industry due to imperfections in clean stock propagation systems, latency of disease development, irrigation systems that allow propagule spread, and a low priority placed on breeding efforts towards Fusarium-resistant cultivars of ornamentals. Management requires a multifaceted approach employing cultivar resistance as well as cultural, biological, and chemical strategies. Ignorance of the sources of inoculum and how it is spread has allowed many missed opportunities for preventing Fusarium wilt diseases. When the disease has become established in a production system, many approaches for achieving suppression have been explored, but most have not met the high standard for a zero disease threshold demanded by the industry. The following review was designed to highlight management studies that have advanced our knowledge of how to minimize Fusarium diseases and to indicate areas where additional research and technological development are needed.

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1. Introduction

The production of ornamental plants increased globally over the last century in both developed and developing countries. Ornamentals include deciduous and evergreen trees, shrubs, foliage plants, cut flowers, flowering potted plants, garden (bedding) plants, potted garden plants, herbaceous perennials and cut cultivated greens. The ornamental production sector has seen rapid changes in the type of product produced, the technology used to produce it, and in the production locations. During the last several decades, hundreds of new crops have been introduced. New products such as potted plants have begun to replace cut flowers, improved techniques have been developed for growing and handling ornamentals, and new locations for producing and marketing ornamentals have dramatically altered the industry. These changes have profoundly influences the management of pests and diseases (Daughtrey and Benson, 2005; Gullino and Garibaldi, 2005, 2006; Gullino et al. 2012b). Given that the standard for ornamental quality is very high, much care in arthropod pest and disease management is necessary, not only to secure yield, but also to meet a high esthetic standard.

Technological changes, such as precise environmental and nutritional controls, have the specific goal of reducing production costs and maximizing profits. However, many of these changes have pushed plants to their limits of growth and productivity. Maximized production systems have generated new stress conditions for crops that are more conducive to many pests and diseases, including Fusarium wilts.

Novelty is another important driver of the ornamental industry. The continual search for new crops and new cultivars has played a major role in this industry. Many genera and species with potential to become economically important crops have been discovered and exploited by an industry that uses newness to catch the fancy of customers with disposable income. The diversity of crops, their cultivars, and their geographic sources, combined with the constant shifts in consumer interests, multiply the number of potential pests and diseases which endanger profits.

Ornamental crops may be grown outdoors, in ground beds (e.g. field tree and shrub nurseries, cut flowers, and flower bulbs) or in containers. Indoor crop production within greenhouses may be on raised benches or directly on the floor. Pots only rarely contain soil: usually container nurseries or greenhouses rely upon soilless

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mixtures based on peat or bark. Some greenhouse businesses use hydroponic systems, such as sand or rockwool culture, or flowing nutrient systems without a matrix for the roots (Gullino et al., 1999). The trend away from cut flowers to potted flowering plants and bedding plants during the latter half of the 20th century led to a big change in the production and transport sectors. Ornamentals production shifted from soil-based media to soilless substrates: lighter growing media reduced shipping cost and also decreased the incidence of soilborne diseases, including Fusarium wilts. This change had some unforeseen side effects—for example, widespread use of media high in organic matter increased the importance of fungus gnats, a new vector for transmission of *Fusarium* (Elmer, 2008).

Most ornamentals produced by the floriculture industry in northern climates are grown in protected and heated glass- or plastic-covered greenhouses. Since the production of ornamentals is very labor-intensive and requires high fuel expenditures in cold weather, one recent industry trend has been a shift away from local plug and rooted cutting production. Today highly desirable annuals and perennials are produced as unrooted cuttings in areas of the world that lack large quantities of customers, but have the advantages of high light and relatively low labor and heating costs. Specialist propagators who root plants that they import as unrooted cuttings then sell to other growers who finish the crop for sale to consumers in Europe and the United States. Some growers in northern climates specialize in the production of plugs of young plants from cuttings or seed, shipping these propagation units to other growers for finishing. This cost-reducing distribution system has led to widespread international and interregional movement of living plants, contributing to the diffusion of pests and pathogens. This situation is especially favorable to the spread of pathogens, such as *Fusarium oxysporum,* that can be moved unseen, as latent infections.

Because of the high capital investment involved in modern greenhouse ornamental production, and potentially high profits, more expensive disease control tactics including reliance on chemicals have been the norm since the 1960s. The high yields and high quality of ornamental crops obtained in this manner have set a standard that is not easy to maintain today now that regulatory limitations on chemical use have reduced the arsenal of effective products. Regulations have been particularly restrictive in Europe. One reason for the many examples of recently emerging Fusarium wilts could be reductions in pesticide use, particularly reduced use of fumigants, in ornamentals production. Other factors may also have contributed to the rise in new Fusarium wilts: more new crops, more intensive cultivation, and the increasingly international nature of trade have all favored the global transmission of *Fusarium* spp. via propagation material.

2. Main crops affected by Fusarium wilts

Fusarium wilts, incited by different *formae speciales* of *F. oxysporum* (Booth, 1984) along with its sister species, *Fusarium foetens*, *Fusarium hostae,* and *Fusarium redolens*, can cause economic losses in a wide range of important crops including ornamentals (Elmer, 2008; Garibaldi, 1978; Wang and Jeffers, 2002). Fusarium wilt can affect and damage ornamental plants at all production stages. Some of the best known of these diseases commonly affect flowering potted plant crops that are often produced in greenhouses. Herbaceous ornamentals that are commonly subject to Fusarium wilts include aster, begonia, carnation, chrysanthemum, cyclamen, gerbera, gladiolus, lily, lisianthus, Paris (Marguerite) Daisy, Persian violet, ranunculus, and tulip. Damage in tulips may include the indirect effect of widespread bulb injury during storage, due to ethylene produced by bulbs affected by basal rot (Munk, 1972). Some woody ornamentals are also affected by Fusarium wilt diseases (Sinclair and Lyon, 2005). Mimosa (*Albizia julibrissin*) and tree-of-heaven (*Ailanthus altissima*) share susceptibility to *F. oxysporum* f. sp. *perniciosum*. Palms may also be susceptible to Fusarium wilts (Canary Island date palm is affected by *F. oxysporum* f. sp. *canariensis*; queen palm and Washington palm by *F. oxysporum* f. sp. *palmarum*). *Fusarium* f. sp. *rhois* is a pathogen of ornamental sumac (*Rhus*) and f. sp. *pyracanthae* and f. sp. *hebe* cause Fusarium wilt on pyracantha and hebe, respectively. A Fusarium wilt caused by *F. oxysporum* has also been reported in proteas grown in South Africa (Swart et al., 1999).

2.1. Carnation

The pathogen *F. oxysporum* f. sp. *dianthi* and its sister species, *F. redolens* f. sp. *dianthi*, continue to cause severe losses wherever carnations are grown, in spite of sanitation practices like routine soil disinfestation prior to each crop and the use of cuttings obtained from *Fusarium*-free meristem tissue cultures (Baker et al., 1985). Severe epidemics of Fusarium wilt in the 1980s and 1990s caused a strong reduction in the acreage devoted to the carnation industry in some areas of Southern Europe, such as Italy, France, and Spain. Fusarium wilt along with cheaper production cost in Colombia, Morocco, Kenya, and Tanzania shifted the industry out of Europe and the United States. Despite the availability of cultivars that are resistant to the most common races of *Fusarium dianthi*, Fusarium wilt remains a critical disease for this crop whenever it is grown (Garibaldi and Gullino, 2012a).

2.2. Chrysanthemum

F. oxysporum f. sp. *chrysanthemi* is the causal agent of wilt of chrysanthemum (Jackson and McFadden, 1961). The causal agent was described as *F. oxysporum* f. sp. *chrysanthemi* by Armstrong et al. (1970). In 1992, two distinct physiological races were described in *F. oxysporum* f. sp. *chrysanthemi* based on the reaction of six differential chrysanthemum cultivars (Huang et al., 2000). More recently, in the Italian Riviera, where cut flowers and potted plants are grown intensively, three new Fusarium wilt diseases incited by *F. oxysporum* f. sp. *chrysanthemi* have been reported in Compositae: on gerbera (*Gerbera jamesonii*), Paris (Marguerite) daisy, (*Argyranthemum frutescens*), and African daisy (*Osteospermum* sp.) (Minuto et al., 2007; Garibaldi and Gullino, 2012b). A study on isolates obtained from these three crops revealed the presence of three physiological races in *F. oxysporum* f. sp. *chrysanthemi* based on different pathogenic reactions on differential cultivars of host species (Troisi et al., 2013). *F. oxysporum* f. sp. *tracheiphilum* race 1 has also been described as the causal agent of Fusarium wilt of chrysanthemum in the United States (Horst and Nelson, 1997) as well as in Italy (Garibaldi and Gullino, 2012b). More recently, *F. oxysporum* f. sp. *tracheiphilum* has been reported on gerbera in Italy and Brazil (Troisi et al., 2009; Garibaldi and Gullino, 2012b).

2.3. Cyclamen

Fusarium wilt of cyclamen (*Cyclamen* L.) occurs wherever the crop is grown commercially. The disease has caused major losses for the industry and was in part responsible for many greenhouse businesses in Europe and the United States abandoning production (Elmer and Daughtrey, 2012). *F. oxysporum* f. sp. *cyclaminis* is the causal agent (Tompkins and Snyder, 1972). No races have yet been identified, but one survey using vegetative compatibility groups and RFLP analysis discovered that three clones exist (Woudt et al., 1995). Although resistance to Fusarium wilt may exist in related

Cyclamen spp., all cultivars of the florist crop are currently considered susceptible (Ewald et al., 2000; Orlicz-Luthardt, 1998; Tompkins and Snyder, 1972).

2.4. Bulb and minor crops

Most bulb crops, including crocus, gladiolus, hyacinth, iris, tulip, lily, narcissus, and ranunculus, are subject to Fusarium wilt caused by different *formae speciales* of *F. oxysporum* (Moore, 1979). Fusarium diseases are more severe in areas that are warm and humid during the growing season, but they also occur in cooler areas—where disease development is slower, and symptoms are reduced (Linderman, 1981). Although Fusarium wilt remains a problem, new tissue-culture technology and propagation systems in Europe have lowered its relative importance (Elmer, 2012a; Gullino, 2012; Gullino et al. 2012a). Fusarium wilts have also been recorded on a number of minor ornamentals, such as agave (*Echeveria agavoides*), begonia (*Begonia* × *hybrida*), Bitterroot (*Lewisia rediviva*), Bloodroot (*Sanguinaria canadensis*), China aster, (*Callistephus chinensis*), coreopsis (*Coreopsis* spp.), flannel flower (*Actinotus helianthi*), hebe (*Hebe* spp.), hosta (*Hosta* spp.), jade plant (*Crassula ovata*), lisianthus (*Eustoma grandiflorum*), Persian violet (*Exacum* spp.), and poppy (*Papaver nudicaulis*) (Bertetti et al., 2013a, 2014, 2013b; Elmer, 2008; Elmer et al., 2007; Elmer and O'Dowd, 2001; Elmer and Marra, 2012; Garibaldi and Gullino, 2012b). The emergence of so many different *formae speciales* of *F. oxysporum* on minor ornamentals over the past 15–20 years may be in part due to the expansion of horticulture into a more international business as well as to the adoption of more intensive cultivation practices.

3. Critical aspects of management strategies for Fusarium wilts

The unique features of the ornamental industry that were previously discussed have a strong influence on disease management strategies. In general, Fusarium wilts are currently managed by a loose assortment of practices held together under the concept of integrated pest management. A more holistic approach and inclusion of all applicable management practices is urgently needed to reduce the economic impact of Fusarium wilts in ornamentals.

3.1. Breeding strategies

Although host resistance is the most effective long-term strategy for managing Fusarium wilt, industry efforts to breed or select ornamentals for disease resistance is virtually absent. At a time of increasing societal concern regarding public health and the environment—and stricter government standards regulating exposure of workers to pesticides—the production of disease-resistant cultivars offers the ideal means to reduce pesticide use without reducing crop quality. However, adoption of this strategy by the industry is hindered because potentially resistant selections that do not meet horticultural performance standards are eliminated. Development of disease resistant cultivars through traditional plant breeding methods has been largely relegated to academia.

Due to the importance of the carnation crop worldwide, breeders have attempted to obtain resistant cultivars that have been tested for their performance under different conditions (Garibaldi and Gullino, 1987; Ben-Yephet et al., 1997). The presence of several races of *F. oxysporum* f. sp. *dianthi* complicates the development and deployment of resistant cultivars (Garibaldi and Gullino, 1987). Resistance to races 2 and 4 appears to be associated with several genes and therefore may be long-lasting (Arus et al., 1992; Blanc, 1983; Demnink et al., 1987; Niemann, 1992). Resistance to race 1 is considered monogenic by Demnink et al. (1987) but not by Baayen et al. (1991), who concluded that resistance to race 1 could be governed by one or several genes. Tramier et al. (1987) suggested the presence of two types of horizontal resistance to race 2: one depending on the inoculum level and another that was more stable and not influenced by inoculum concentration. Ben-Yephet et al. (1997) identified two carnation cultivars showing monogenic resistance to race 2 of *F. oxysporum* f. sp. *dianthi*. Being that race 2 is the most widespread, the presence of cultivars resistant to it would be very useful for growers (Garibaldi and Gullino, 2012a).

In the case of bulb crops, cultivars vary in susceptibility to Fusarium wilt. For gladiolus, the degree of tolerance of some cultivars is sufficient for growers to be able to control the disease with corm dips (Elmer, 2006a; Magie, 1985). Most research into Fusarium resistance in bulb crops has been carried out in the Netherlands, due to the economic importance of the cultivation of flower bulbs in that country. Van Eijk and Eikelboom (1983) produced reliable screening tests for tulips. Nearly absolute resistance was found within the *Tulipa gesnerianus* assortment (Van Tuyl and van Creij, 2007). In the case of lily, a high degree of resistance was found in some Asiatic cultivars and in some species, such as *Lilium dauricum*, whereas Oriental hybrids were susceptible (Straathof and van Tuyl, 1994; Straathof et al., 1996).

No resistance was seen in an unspecified number of seedlings of cyclamen tested from different seed lots by Tompkins and Snyder (1972). Orlicz-Luthardt (1998) and Ewald et al. (2000) identified tolerance in related species and interspecific hybrids of *Cyclamen persicum* Mill. × *Cyclamen purpurascens*. For chrysanthemum, resistant cultivars are well known (Englehard and Woltz, 1971; Garibaldi et al., 2009). Many cultivars of Paris daisy (*Argyranthemum frutescens*), African daisy (*Osteospermum* sp.), and gerbera (*G. jamesonii*) have recently been shown to be resistant to Fusarium wilt incited by *F. oxysporum* f. sp. *chrysanthemi* (Garibaldi et al., 2009; Gullino and Garibaldi, 2006). Only limited information exists on the availability of resistant cultivars for minor ornamentals. In the case of *Hebe*, most species (*H. odora*, *H. amplexicaulis*, *H. bollonsii* × *H. lewisii*, *H. mattewwisii*, *H. salicifolia*) are susceptible to *F. oxysporum* f. sp. *hebae*. Only *H. cupressoides* is not susceptible to the pathogen (Raabe, 1985).

For Fusarium wilt of lisianthus (*Eustoma grandiflorum*), a screening was carried out on the most popular cultivars grown in Italy which revealed that the cvs. Mariachi Green and Echo Dream Yellow were partially resistant to the disease (Gilardi et al., 2006). In the case of Fusarium wilt of *Protea*, variability in susceptibility to Fusarium wilt among cultivars has been observed (Swart et al., 1999), suggesting further selection may increase host resistance.

Over the years there have been periodic screenings of local cultivars and selections of China asters for resistance to Fusarium wilt (Elmer and McGovern, 2013; Jones and Riker, 1931; Riker and Jones, 1935). However, the appearance of new races of the pathogen has lowered hopes of achieving any durable, lasting resistance. A recent screening of 44 cultivars found that only four had moderate resistance in field trials (Elmer and McGovern, 2013).

The availability of resistant cultivars for most hosts is sparse, and there is a need for further research in this field, so that growers are provided with a certain degree of choice. Plant breeders should recognize that new cultivars chosen for other desirable traits may exhibit more susceptibility to Fusarium wilt rather than less. For example, new ranunculus F1 hybrids were found to have more susceptibility to Fusarium wilt than the old cultivars (Gullino and Garibaldi, 1985). Also, disease resistance is not always complete and can be overcome by conditions very favorable to disease development or by the appearance of new races of the pathogen. Nevertheless, disease resistance remains a key component within an IPM framework, and it will likely be increasingly important in

the future.

3.2. Cultural practices

New technologies for the production of ornamentals have given growers some powerful management tools. Many of these have significantly affected the epidemiology or severity of Fusarium diseases. The controlled environment of a greenhouse furnishes growers with opportunities to ensure that the plants, the growing media, and greenhouse materials and surfaces are initially free of pathogenic *Fusarium* spp. Field growers do not have this advantage. Plant density can influence disease severity in either environment because Fusarium pathogens have limited ability to grow in soil—thus spread of the disease to adjacent plants appears to be from root to root (Price, 1975). Reducing the incidence of wounds and bruises while digging, cleaning, and grading can be important for disease control in bulbs, because infections may occur if healthy and diseased bulbs come in contact with one another (Price, 1975). The same is true for other perennial plants, such as hosta: wounding during divisions may result in disease spread unless careful sanitation practices are employed (Wang and Jeffers, 2002). Proper cultural techniques may help to reduce wilt attacks. For example, cultivating carnations in isolated, raised benches or in soilless systems permits better soil/substrate disinfestation, lowering the pathogen inoculum compared to ground beds. Switching to raised benches was so effective that in France, where carnation cultivation had high economic value in the 1980's, governmental support for adopting raised bench cultivation was made available (Garibaldi and Gullino, 1987).

Changes, such as the use of hydroponic and soilless cultures, artificial substrates, flooded floors, and computerized systems have dramatically altered the way many ornamentals are produced. More precision in environmental and nutritional control has pushed productivity to new levels. As a result, unexpected outbreaks of Fusarium diseases can occur where none were observed before the change. For example, wilt of gerbera caused by *F. oxysporum* f. sp. *chrysanthemi* was surprisingly shown to be more severe on plants grown in soilless systems than in soil (Garibaldi and Gullino, 2012b).

3.3. Sanitation

Sanitation represents the first and most effective strategy against Fusarium wilts under greenhouse or nursery conditions. It includes the use of soil and substrates disinfested with steam, fumigants, or solarization (Gamliel and Katan, 2012). Determining where and how the inocula of *Fusarium* pathogens persist in the greenhouse is paramount to their eradication. Given the known persistence of *Fusarium* propagules, growers should assume that anything in the greenhouse could potentially harbor inoculum. There are several sanitary measures that can be performed, well before the new crop cycle begins, to eliminate inoculum and reduce the incidence of future outbreaks. Infected plant residues and infested soil that remain on the greenhouse floor, on support strings, trays, pots, and utensils can provide reservoirs of inoculum. Use of foot baths at access doors can prevent *Fusarium*-infested soil and debris from entering the production facilities. Short or no rotations of greenhouse crops can allow build-up of *F. oxysporum* populations if the soil is not disinfested between production cycles.

Conidia of *Fusarium* pathogens on an infected crop may become airborne and contaminate greenhouse structures (Rekah et al., 2000; Rowe et al., 1977). Treating greenhouse structures, pots, trays, and bench tops with environmentally safe disinfestants, such as hydrogen peroxide or chlorine dioxide-based products, can reduce inoculum on surfaces. However, it is also important to prevent recontamination, which requires an understanding of how Fusarium conidia spread in each system. A relatively new challenge for greenhouse growers has been sanitizing recycled irrigation water. Several methods have been studied, including activated hydrogen peroxide, chlorination, heat treatment, iodination, membrane or slow sand filtration, ozonation, and ultraviolet (UV) radiation. Activated hydrogen peroxide and peracetic acid formulations disinfested irrigation contaminated with *F. foetens* (Elmer et al., 2014). Slow sand filtration was effective in reducing inoculum of *F. oxysporum* f. sp. *cyclaminis* to 0.1% of its original value (Runia, 1995).

3.4. Seed and propagation material disinfestation

When greenhouses are free of *Fusarium* pathogens, care must be exercised to prevent their re-entry. It is easy to introduce Fusarium diseases for which the pathogen is known to be transmitted on seeds and seed debris, such as cyclamen wilt (Tompkins and Snyder, 1972)—or on propagation material, as shown for wilts of carnation, bulb crops and members of the Asteraceae (Garibaldi and Gullino, 2012b). Tests of propagation material for *Fusarium* spp. are only performed in rare situations because contamination is usually present only on a very low percentage of seeds or cuttings and thus is easily missed when only samples are tested. When China aster (*C. chinensis*) seeds were placed on a selective medium, Elmer and McGovern (2013) found that seven out of 25 commercial seed packages contained seeds infested with *F. oxysporum* f. sp. *callistephi*. Since all Fusarium diseases have the potential to be seedborne, growers should assume that their seeds and propagation material are possible sources of inoculum, regardless of whether or not seed transmission has been reported previously for a given host–pathogen combination. Numerous disinfectants could theoretically be used for seed disinfestation, including $NaHClO_2$, hydrogen peroxide, quaternary ammonia compounds, various alcohols, and organic solvents with fungicides. Unfortunately, reliable seed and propagation material disinfestation protocols have not been developed for most crops. A brief exposure with agitation in diluted household bleach was shown to eradicate 95–99% of *Fusarium* spp. in China aster seed (Elmer and McGovern, 2013). However, seed of other species might be more effectively decontaminated with hot water treatment. The addition of surfactants might improve effectiveness of surface disinfestants. For years, bulbs were treated by dipping in fungicides, mainly benzimidazoles, which were effective not only against *F. oxysporum,* but also against *Penicillium corymbiferum*, the causal agent of another bulb rot. However, resistance to benzimidazole chemistry quickly developed (Garibaldi and Gullino, 1990). In response to this problem, other fungicides, such as dichloran, chlorothalonil, and captan, were at first combined with benzimidazoles to reduce the spread of benzimidazole resistance (Magie and Wilfret, 1974). Later, prochloraz dips replaced benomyl dips (Garibaldi and Gullino, 1990; Migheli and Garibaldi, 1990). Today, however, very few fungicides are registered for suppressing Fusarium diseases on bulbs, corms, or rhizomes despite research showing such dips can be effective (Elmer, 2006a).

Interesting results in disease control have also been achieved in the case of gladiolus, iris, and tulip with hot water treatments, either alone or in combination with reduced dosages of fungicides (Magie, 1985; Garibaldi and Migheli, 1988; Migheli and Garibaldi, 1990). The temperatures used vary according to the host, utilizing 49 °C in the case of gladiolus, up to 52 °C in the case of small gladiolus corms, and 55 °C for cormels (Magie, 1985). Cohen et al. (1990) achieved eradication of *F. oxysporum* f. sp. *gladioli* propagules by hot water treatment for 30 min at 57 °C. Roebroeck et al. (1991) developed a mathematical model for the hot water

treatment of gladiolus, showing 5% and 99% death of corms and *F. oxysporum* f. sp. *gladioli* conidia, respectively. Hot-water formaldehyde treatments were once carried out to suppress Fusarium diseases on narcissus (Chastagner and Byther, 1985). When hot water treatment was combined with low dosages of a benzimidazole, a synergistic effect was detected in gladiolus and iris (Garibaldi and Migheli, 1988; Migheli and Garibaldi, 1990). Chlorine dioxide proved effective in inhibiting conidia of *F. oxysporum* f. sp. *narcissi* (Copes et al., 2004). Recently, ultraviolet C (UV–C) radiation at low doses has emerged as an alternative technology to avoid the use of fungicides. Sharma and Tripathi (2008) controlled Fusarium rot of gladiolus corms by integrating the use of hot water and low dosages of UV-C.

3.5. Rotation to new land

Many ornamentals are grown in field operations where build-up of Fusarium inoculum over time becomes problematic. Where new land is available, rotation offers the time-honored practice of eliminating the pathogen along with many other pest issues. However, when the intent of the grower is to return to the land within five years, the anticipated benefits of crop rotation may not be realized. The Fusarium wilt pathogens possess the ability to colonize and produce inoculum on resistant cultivars or rotation crops, so rotation may not be an effective practice (Elmer, 2012a; Elmer and Lacy, 1987; Scott et al., 2013).

3.6. Suppressing insect vectors of Fusarium propagules

Insects, most notably fungus gnats (*Bradysia* spp.) are vectors of *Fusarium* spp. in greenhouses and nurseries (El-Hamalawi and Stanghellini, 2005; Elmer, 2008; Gillespie and Menzie, 1993; Keates et al., 1989). Elmer (2008) showed that healthy begonias caged with plants infected with *F. foetens* became diseased when fungus gnats were present, but remained healthy when fungus gnats were suppressed with imidacloprid insecticide. The advent of soilless potting mix has had the negative consequence of providing habitats that are very favorable for fungus gnats. Thus, new management strategies are needed by ornamental growers for suppressing *Fusarium* spp. and other pathogens as a result of this switch to soilless potting mixes.

3.7. Culture-indexing

This technique was first suggested for the detection of Fusarium wilt of carnation at the end of the 19th century (Mangin, 1899). Forty years later, the plate method was developed for routine screening of chrysanthemum cuttings for vascular wilt fungi (Dimock, 1943). This procedure involved incubating small, surface-disinfested pieces of basal stem cuttings taken from asymptomatic stock plants on potato-dextrose agar (PDA) and observing for the growth and appearance of *Fusarium* colonies. Although the technique was modified extensively by others (Nelson et al., 1960; Tammen et al., 1956), it still only provided marginal assurance that cutting stock was free of these pathogens. Pathogen-free propagation programs have been routinely adopted for major ornamental crops, especially for chrysanthemums. Several researchers, however, found the culture-indexing assay to be ineffective and result in false negatives, possibly due to failure to follow the strict guidelines, the low incidence of contaminated cuttings, or interference from other competing microorganisms that suppressed the growth of *Fusarium* spp. (Tammen et al., 1956). Another explanation for false negatives could be due to the manner in which *Fusarium* spp. colonize host vascular tissue. Fisher and Toussoun (1983) found that chrysanthemum stock that was judged clean by culture-indexing was discontinuously colonized by *F. oxysporum* f. sp. *chrysanthemi*. Apparently, conidia were produced and dispersed in the vascular tissue ahead of the advancing mycelium, so that infections could occur above the portion of the stem that was cut to check for contamination. Although the assay is still in use for a wide array of plant pathogens, its ability to detect *Fusarium* spp. is still insufficient (Raju and Olson, 1985). Developing plants from apical meristems via tissue culture before culture indexing provided much better assurance that stock material was clean from bacterial and fungal pathogens; viral contamination could also be addressed by adding heat treatment prior to taking meristems (Worfolk and deLacy, 1986).

3.8. Nutrition

Manipulation of fertilization practices offers unique opportunities to influence the development of Fusarium wilt given that growers have control over fertilization. The use of liquid fertilization in soilless mixes or hydroponic culture allows for precise control that may be adjusted as necessary during the crop cycle. Six elements—nitrogen, calcium, chlorine, iron, manganese, and zinc—have been sufficiently researched to conclude that their application can directly affect development of Fusarium wilts and root rots (Elmer, 2012b). These elements in some cases alter the physiology of the host or pathogen and alternatively may increase the effectiveness of biocontrol agents (Datnoff et al., 2007a). However, until precise disease-suppressive fertilization regimes are developed for each pathosystem, only generalities can be discussed.

With very few exceptions, Fusarium diseases on greenhouse crops are suppressed by nitrates (Huber and Thompson, 2007; Jones et al., 1989). Engelhard and colleagues (Engelhard, 1975, 1979; Engelhard and Woltz, 1973) compared NH_4NO_3 to $Ca(NO_3)_2$ on asters, carnations, and chrysanthemums and determined that $Ca(NO_3)_2$ was consistently more suppressive to Fusarium wilts than ammoniacal forms of nitrogen. Many of the underlying mechanisms by which nitrate governs disease suppression are related to the pH of the root medium. These effects occur through chemical reactions in the potting mix as well as root-mediated ion exchanges near the roots. Exceptions do occur: carnation wilt severity is decreased by ammonia–nitrogen as compared to nitrate–nitrogen—and the effect of high pH and ammonia–nitrogen fertilization may be additive, resulting in enhanced wilt reduction (Pergola et al., 1979). According to Loffler et al. (1986), nitrite rather than ammonia is responsible for the population-reducing effect on *F. oxysporum* f. sp. *dianthi* in the soil. This effect has been explained by decreased chlamydospore formation and enhanced lysis of chlamydospores by nitrites. Soil amendment with sulfur or peat decreases soil pH, thus favoring the appearance of wilt symptoms. Nitrogen rate can also affect disease: higher rates increased wilt development on carnation (Gasiorkiewicz, 1960).

On bulb crops, the inoculum potential of *F. oxysporum* can be adjusted through the use of different soil fertility regimes. Keeping the soil pH at 6.5 to 7.0 and applying nitrate forms of nitrogen are good practices for counteracting Fusarium wilt on these crops. More acidic reactions are associated with disease development (Nelson et al., 1981), and the use of potassium decreases disease (Chastagner and Byther, 1985).

Applying calcium (as lime) to the root medium to raise pH can also suppress Fusarium wilts (Engelhard, 1979; Engelhard and Woltz, 1973; Jones et al., 1989). A soil pH of 7.5 or higher decreases Fusarium wilt disease severity on carnation (Garibaldi and Gullino, 1987). The role of calcium itself in the management of plant disease has received much attention, but there are few examples for ornamental crops. Many previous studies that investigated the role of $Ca(NO_3)_2$ credited the plant disease suppression to the

nitrate ion and failed to recognize the calcium ion. However, during any stage of development of carnation, a shortage of calcium increases disease severity. Any cultivation practices that lead to calcium deficiency could contribute to increased disease severity (Blanc et al., 1983), but obviously, the root zone interactions between calcium, pH, and the pathogen are far more complex than the matter of satisfying the nutritional requirement for calcium (Elmer, 2012b).

Although chlorine is routinely applied as a chloride in fertilizers, its role in Fusarium disease suppression is poorly understood (Elmer, 2007). Research on the beneficial effects of chlorine is rare, especially when the impacts of accompanying ions are considered and accounted for. For example, conflicting reports in field crops on the benefits of potassium nutrition frequently depend on whether potassium was applied as KCl or K_2SO_4 (Sanogo and Yang, 2001). Most greenhouse and field studies where chlorine nutrition is examined are conducted with sodium and high levels of salinity; thus, negative effects on crops are often generated (Triky-Dotan et al., 2005). Cyclamen plants inoculated with *F. oxysporum* f. sp. *cyclaminis* and exposed to chloride salts were larger and had fewer symptoms of disease than plants that received no chlorine (Elmer, 2002). Although this chlorine amendment strategy might be useful with additional crops, we need more information on how to identify responsive plants and how best to apply chlorine.

Micronutrients can also affect the development of Fusarium disease. They can favor the pathogen and subsequently increase disease, or provide essential nutrients to bioantagonists or to the host plant that assist in its defense. As the root medium approaches neutral pH and their availability are reduced, micronutrients can become limiting for *Fusarium* spp. (Duffy, 2007; Expert, 2007; Huber and Thompson, 2007). The latter scenario may be one mechanism by which adding lime or nitrate affects Fusarium diseases. Most plants have the ability to extract and absorb micronutrients using root-mediated chelating metabolites, even at neutral pH, and many beneficial microbes that are applied for biological control also increase the availability of micronutrients. Nonetheless, one should never underestimate the need which greenhouse plants grown in soilless culture have for micronutrients. Metals are cofactors or activators of enzyme systems that play pivotal roles in the production of defense products in plants. The levels of micronutrients needed to ensure proper plant health and defense against disease can be lacking in soilless mixes even though visual deficiency symptoms may be absent. Although aboveground deficiency symptoms can be easily corrected with foliar applications of these nutrients, these applications are not translocated to the roots and, thus, do not protect against root infections. Prescribed applications to soil to optimize and balance micronutrient fertility in order to increase protection from Fusarium disease should be examined in future research. Silicates, which proved effective against Fusarium wilts of vegetable crops, could perhaps be utilized for some ornamentals (Datnoff et al., 2007b). Many ornamental grasses are high accumulators of silicon. Given that silicon is usually deficient in most potting mixes, the opportunity to enhance disease resistance to Fusarium root rot and wilts with silicate amendments deserves attention.

3.9. Organic amendments

During the past three decades, various composted organic wastes have partially replaced peat in container media used for the production of ornamentals. These wastes are now being recycled for both economic and production reasons (Noble and Coventry, 2005). The cost of composts can be lower than that of peat. Some compost-amended media, especially those with composted hardwood bark, will suppress major soil-borne plant pathogens and thus reduce plant losses and production costs (Hoitink and Boehm, 1999; Hoitink and Locke, 2012). Many researchers have shown this disease-suppressive effect of composted bark against Fusarium wilt on ornamentals (Garibaldi, 1984; Hoitink et al., 2001). Although composts may not control diseases to a level that will replace the use of fungicides, their integration into current disease management practices may reduce fungicide use. Various types of organic substrates (sphagnum peat, bark, composts, coir, rice hulls, etc.) may contribute to disease suppression, but favorable results have been reported most often from the use of compost amendments (Hoitink and Boehm, 1999; Scheuerell et al., 2005; Termorshuizen et al., 2007). When hardwood bark (composted or not) is used, improved plant growth is observed, especially in potted plants. Disease suppressiveness and improved vigor of plants in such bark substrates result from both the physical characteristics of bark composts and from the higher levels of antagonists that they support (Hoitink and Boehm, 1999). Although in most cases composted materials have been used in container media (De Ceuster and Hoitink, 1999; Hoitink et al., 2001), there are also several references in the literature on the use of composted materials to suppress soil-borne plant diseases of turfgrass (Noble and Coventry, 2005). To improve the consistency of disease control using composts, biological control agents have been added to compost amendments: composts can provide a food base for these agents against soilborne pathogens (Ramona and Line, 2002).

3.10. Chemical control

In recent years, the number of chemicals registered for use on ornamentals has sharply decreased, forcing growers to exploit other control measures. Also, the cost of generating efficacy and phytotoxicity data for the large number of ornamental plant species discourages chemical companies from expanding the labels of new materials to include these crops (Gullino and Garibaldi, 2005). Pesticide residues diminish retail value of treated plants and frequent use of pesticides often hardens, marks, or stunts some, if not all, cultivars of a species. These considerations, combined with incomplete effectiveness of chemical treatments against Fusarium wilts, have made chemical control disappointing for growers.

In bulb crops, resistance to benzimidazoles is widespread in *Fusarium* pathogens causing bulb rot and wilt. This loss of effectiveness for traditional bulb and corm dips has caused some problems because other effective fungicides are sometimes phytotoxic (Gullino and Garibaldi, 2005). In some countries, prochloraz and azoxystrobin replaced benomyl for the control of several Fusarium wilts of ornamentals, including Fusarium wilt of carnation (Gullino et al., 2002; Garibaldi and Gullino, 2012a,b) and bulb crops. Prochloraz has never been registered for ornamentals in the United States, however, and the pricing of azoxystrobin has limited its use on many bulb crops (Chase, 2012).

One test on lisianthus found that materials containing fludioxonil were more effective against Fusarium wilt than strobilurin treatments or bioantagonists: symptoms developed in all of the inoculated controls, but in only 36–42% of the fludioxonil treated plants (McGovern et al., 2002a). A second trial comparing fungicides showed the best reduction in disease incidence from applications of triflumizole and fludioxonil, which outperformed benzimidazole, strobilurin and myclobutanil treatments (McGovern et al., 2002b).

Due to the great number of cultivated species and cultivars, phytotoxicity remains a major problem for chemicals used in ornamental crops. Integration of chemical fungicides with other control methods has been extensively tested. Using biocontrol agents following fungicides in various combinations has resulted in significant disease control: fludioxonil paired with various

biologicals (including fungal, actinomycete and bacterial agents) yielded the best results against Fusarium wilt of cyclamen (Elmer and McGovern, 2004). The combination of hot water treatment with fungicide treatment has provided interesting results in the case of bulb crops. Chemical treatments alone are not always effective for gladiolus. Thus, gladiolus producers have sometimes prepared corms with a hot fungicide treatment immediately prior to planting, thus combining two methods for greater effect. Unfortunately, the difference in sensitivity of some cultivars to the heat makes use of this method somewhat difficult.

Fungicide treatments used alone on gladiolus have brought disappointing results in recent US trials. No improvement in plant growth or reduction in the percentage of gladiolus corms infected with *F. oxysporum* was reported when corms were dipped in fungicide (fludioxonil or carbendazim) followed by a soil treatment one week after planting (azoxystrobin, chlorothalonil, fluazinam, or trifloxystrobin) (Elmer and McGovern, 2004). Thiophanate-methyl, azoxystrobin, fludioxonil, or triflumizole used first as a corm soak and later as a soil treatment were also ineffective (Elmer and McGovern, 2004). A study looking at acibenzolar-S-methyl (ASM) [a systemic acquired resistance (SAR) material] in combination with fungicides indicated that the ASM at the rates tested was stressful to the plants, sometimes with the result of increased disease (Elmer, 2006b, 2007).

3.11. Biological control and natural compounds

Biological control can indeed represent a breakthrough in the science of Fusarium management. Soils that are suppressive to *F. oxysporum* f. sp. *dianthi* have been described in the United States, France, and Italy (Baker and Linderman, 1979; Garibaldi et al., 1989; Tramier et al., 1983). In all cases, suppressiveness had a microbiological origin that was destroyed by steaming. Certain bacteria or fungi indigenous to these soils have been shown to be responsible for suppression of Fusarium wilt pathogens. The most efficient were identified as *Pseudomonas* and *Alcaligenes* spp. in the United States and as non-pathogenic *Fusarium* species in France and Italy. Antagonistic *Fusarium* spp. isolated from the rhizosphere of carnation plants grown in suppressive soils showed high rhizosphere competence as compared with saprophytic non-antagonistic *Fusarium* spp. isolated from the same soils (Garibaldi et al., 1989); when applied to soil and substrates, they controlled Fusarium wilt on crops such as carnation, cyclamen, and bulb crops (Garibaldi and Gullino, 1990; Minuto et al., 1995; Postma and Rattink, 1992). Strains of *Trichoderma viride* showed good antagonistic activity against Fusarium wilts and have been used in chrysanthemum (Singh and Kumar, 2011). Commercial preparation of beneficial microbes were only marginal in suppressing Fusarium wilt on gladiolus (Elmer, 2006b), but when combined with fungicides, they provide superior control of Fusarium wilt of cyclamen than fungicides alone (Elmer and McGovern, 2004). Microbial optimization of the nutrient solution through the addition of beneficial microorganisms has been successfully attempted for *Phytophthora cryptogea* on gerbera (Garibaldi et al., 2003). The addition of antagonistic organisms could be an interesting approach for management of Fusarium wilts. Biocontrol agents are expected to play a major role in disease management in the future, through better integration into production systems (Fravel, 2005). Speficin combination.

Salts, plant extracts, and oils, such as thyme oil, are increasingly used in gardens and even under commercial conditions to control fungal diseases (Singh and Kumar, 2011). However, trials carried out with plant extracts (Bowers and Locke, 2000) or sodium chloride (Elmer, 2002) against Fusarium wilts of greenhouse crops have obtained only a marginal effect.

3.12. Temperature

Manipulating temperature has only limited use for suppressing Fusarium wilt given that temperature affects crop production time and quality. Because optimal temperature for root infection by *Fusarium* spp. is usually the same or very close to the optimal temperature for plant production, it would be impossible to alter temperature to suppress infection. However, temperature was used to affect the development of symptoms (Ben-Yephet et al., 1994; Gardiner et al., 1987). By lowering greenhouse temperatures, the severity of symptoms on established plants can be reduced, and the development of disease slowed. In the case of Fusarium wilt of carnation, symptoms were absent at 18 °C despite the roots being infected with *F. oxysporum* f. sp. *dianthi* (Ben-Yephet et al., 1994). On the other end of the spectrum, heat extremes increase the onset of Fusarium wilt symptoms in cyclamen (Elmer and Daughtrey, 2012). Hot temperature extremes for Fusarium wilt susceptible crops should be avoided by using shade cloth in the greenhouse, and by avoiding dark-colored pots. Maintaining cool temperature is also important during the storage of flower bulbs.

Fusarium root and crown rot disease of container-grown hostas, incited by *F. hostae*, was affected by temperature: disease severity was higher on plants grown at moderate (18 or 25 °C) temperatures than on those grown at 32 °C, possibly because of negative effects of higher temperatures on the pathogen (Wang and Jeffers, 2002). The researchers suggested that, as a disease control measure, handling and wounding of the crop for propagation purposes might be done at times of the season when temperature would be naturally inhibitory.

3.13. Diagnostic tools

It is realistic to assume that for the purpose of free trade and because of consumer demand, international trade in ornamental products will increase. Inspectors will need to submit fungus-infected material for laboratory diagnosis. As they examine ornamental crops produced from around the globe, the testing laboratories will increasingly identify new pathogens with scientific names other than those now appearing on quarantine-pest lists in phytosanitary regulations. With heightened international biosecurity and biodefense investment, it is expected that the development of new technologies will provide new, more effective, quicker and less labor-intensive methods for detecting and identifying pathogens. Advances in molecular-based diagnostics have already had a strong impact on plant disease management. New diagnostic methods will gradually be utilized by extension services and large propagation companies as well as regulatory agencies and university diagnostic laboratories. Although PCR (polymerase chain reaction) was developed in the 1980s, PCR technology is just beginning to be applied for routine plant diagnosis. Portable real-time PCR instruments are now available (Schaad et al., 2003). Advanced molecular methods have been developed for typing various Fusarium wilts, and these should be very useful for properly identifying and tracking problems in the ornamentals industry. Such methods are also very useful when regulatory control measures are required.

4. Summary

Ornamental growers have a lower threshold of tolerance for disease damage than growers of many other crops. Production costs may be very high, and yields of aesthetically attractive ornamentals must be high as well for businesses to survive. Plant losses to Fusarium wilts cannot be tolerated in modern production. In many cases, management practices to suppress *Fusarium* have a greater

chance of success in the greenhouse than in the field, since more control can be placed on the substrate, irrigation, and temperature components of the production system. The many strategies discussed above can be incorporated into a multifaceted disease management program involving sanitation and nutritional, environmental, biological, and/or chemical approaches. Continued evaluation of these and new strategies is still urgently needed to identify knowledge gaps and opportunities for producing ornamentals that are free from Fusarium wilt diseases.

We proposed the specific areas where research should focus are plant breeding, sanitation technology, improved chemistries and bioantagonists, nutritional influences on disease, and more sensitive and affordable diagnostic assays. As technological advances in gene transfer improved, we expect to identify specific resistance genes in ornamentals that may be incorporated into horticulturally acceptable stock. New technology with flooded floors and ebb and flood irrigation requires us to take a closer look at how to halt the spread of *Fusarium* in irrigation water. Newer formulations of disinfectants need evaluation. Although we recognize that industry will focus on developing fungicides for large acreage crops, development of new chemistries for Fusarium disease and subsequently testing and registration for highly valued ornamentals should follow. Prescriptions for nutritional regimes with N-form, Ca, Cl, Si and micronutrients that optimize growth and also disease suppression are needed for most ornamentals—these may, in the long term, provide a very simple and inexpensive means for enhancing crop health. Still, the enormous amount of time and financial resources required to generate this information may prevent this strategy from being realized until industry awareness of the threat of Fusarium diseases and subsequent funding sources appear. Lastly, we would strongly promote improvement in DNA-based diagnostics to detect latent Fusarium infections in seeds, seedlings, plugs, and cuttings. When assay kits are readily available and affordable to off-shore and local producers along with growers and diagnosticians, faster and more accurate assessments can be made, increasing growers' opportunities for meaningful action.

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