EVOLUTION OF OUR KNOWLEDGE OF *FUSARIUM* DISEASES IN FOREST NURSERIES

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ABSTRACT

Fusarium spp. are recognized throughout the world as very important pathogens in forest nurseries. Diseases caused by *Fusarium* spp. are often the most important factors limiting production of high-quality seedlings in western North America. Initial investigations concentrated on disease etiology and development of direct chemical control procedures. Later work focused on disease epidemiology and the role of environmental factors in disease severity. Several different morphologic species of *Fusarium* are routinely encountered in forest nurseries because they commonly colonize soil and seedling tissues. Within seedlings, they may either elicit disease symptoms or exist as endophytes. *Fusarium oxysporum* and *F. proliferatum* are the most important pathogenic *Fusarium* species within western North America nurseries on bareroot and container seedlings, respectively. Successful reduction of disease losses uses an integrated approach involving cultural manipulations and biological and chemical control. Control efforts seek to reduce pathogen inoculum within seedling growing environments and improve seedling vigor to reduce disease expression. Preventing disease is usually much more successful than therapeutic approaches. Recent studies indicated that pathogenic and non-pathogenic isolates of *F. oxysporum* within forest nurseries are probably genetically distinct. Identifying genetic markers and subsequent development of molecular probes may improve disease severity prediction within forest nurseries by quantifying pathogenic *Fusarium* populations and be useful in screening, evaluating, and producing effective biological controls.

INTRODUCTION

Diseases are important factors limiting the production of high-quality seedlings in forest nurseries throughout the world. When serious investigations into forest nursery diseases began early in the 20th century, *Fusarium* spp. were often found associated with diseases. Investigations in North America initially dealt with pre- and post-emergence damping-off and identified several *Fusarium* taxa that were commonly isolated from diseased seeds and young seedlings (HARTLEY, MERRILL 1918, RATHBUN 1918). Subsequent work evaluated pathogenic potential of several Fusaria and indicated that several species were capable of causing diseases (RATHBUN-GRAVATT 1925, TINT 1945a). After identifying the importance of *Fusarium* spp. in nursery disease etiology, steps were taken to ameliorate pathogen effects, particularly drenching diseased seedbeds with chemical pesticides (WARCUP 1952). Research into *Fusarium* diseases in the 1940s revisited aspects of disease etiology as well as focusing on environmental factors affecting disease expression and severity (TINT 1945b, c). In particular, temperature and soil effects were carefully evaluated and recommendations formulated to reduce disease losses.

The next important phase of research in North America dealing with *Fusarium* diseases in forest nurseries was the series of outstanding investigations conducted by BLOOMBERG (1981, 1985), and VAARTAJA and others (VAARTAJA 1967, VAARTAJA, BUMBIERIS 1967, VAARTAJA, CRAM 1956)

conducted in the 1950s - 1970s. This work focused primarily on diseases incited by *Fusarium oxysporum* SCHLECHT. on bareroot Douglas-fir (*Pseudotsuga menziesii* FRANCO). Research dealt with infection biology, symptom production, disease epidemiology, pathogen biology, environmental effects on disease severity, investigation of disease control, and formulation of an epidemiological model for the disease. All of this work laid the foundation for later work on *Fusarium* diseases, particularly in North America.

Subsequent to this work, significant contributions to our understanding of *Fusarium* diseases in forest nurseries were concerned with disease descriptions on different nursery crops, environment-host/pathogen interactions, interactions between mycorrhizal fungi and *Fusarium* pathogens, potential use of biological control agents to reduce disease severity, and improvement of disease control, particularly by refining pesticide applications and implementing pre-plant soil fumigation or solarization. Noteworthy important research contributions outside North American included work in Japan and Europe (LILJA et al. 1992, MATUO, CHIBA 1966, PROCHAZKOVA 1991).

When workers first started investigating *Fusarium* diseases, difficulties in taxonomy of the genus became evident. Several monographs (BOOTH 1971, GERLACH, NIRENBERG 1982, JOFFE 1974, SUMMERELL et al. 2003, TOUSSOUN, NELSON 1968) have been prepared that deal with *Fusarium* speciation and acceptance of specific treatises by researchers has varied. Some taxonomy resulted in very few species, whereas other work divided the genus into many different taxa (GERLACH, NIRENBERG 1982). During the course of our work on *Fusarium* diseases, we have consistently used the taxonomy of NELSON et al. (1983), primarily because the morphological characteristics used in this treatise are easily recognizable, consistent (particularly if isolates are processed and maintained in particular ways), and accepted by many *Fusarium* researchers (SUMMERELL et al. 2003).

Morphological differentiation of taxa may not necessarily reflect actual phylogeny (GORDON, MARTYN 1997, KISTLER 1997, O'DONNELL et al. 1998). As a result, new taxonomy of some *Fusarium* sections have been developed using molecular genetics (NIRENBERG, O'DONNELL 1998, O'DONNELL et al. 1998). These probably more accurately reflect true phylogeny of these organisms than traditional morphological characterization. However, molecular techniques are currently not available to all workers dealing with this important pathogen genus. Therefore, reliance on morphology will be necessary until molecular differentiation can be routinely used by most investigators (SUMMERELL et al. 2003).

Our work on *Fusarium* diseases in forest nurseries began many years ago, primarily in response to problems in newly-established container seedling facilities. Container seedling production became more important starting in the early 1980s, particularly within the Inland Pacific Northwest. However, *Fusarium* diseases were devastating in some nurseries, even to the point where nearly entire crops were lost to these diseases (JAMES, GILLIGAN 1984). Although our work initially involved pathogen identification and recommendations for reducing disease impacts, we found that important biological questions regarding behavior of *Fusarium* spp. in container nurseries needed answers. Therefore, we initiated research into these diseases in container nurseries. Most of the remainder of this paper summarizes this work. In addition, we summarize recent work we have been involved in concerning initial findings about molecular characterization of *Fusarium oxysporum* populations and differentiation of pathogenic from non-pathogenic isolates of this species within forest nurseries.

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Fusarium causes several types of diseases throughout the growth cycle of container-grown seedlings. Pre- and postemergence damping-off are usually caused by *Fusarium* residing on or, less frequently, within seeds (DUMROESE et al. 1988, JAMES 1984c, 1985c, 1986a, b, 1987c, 1999). The most important damping-off species is *F. oxysporum* (JAMES 1984a, 2004b, JAMES et al. 1991), although several other *Fusarium* species are routinely isolated from conifer seeds (JAMES 1986a, 1987d). Most *Fusarium* contaminate seedcoats and infect emerging radicles during germination (JAMES 1986a, JAMES, GENZ 1981, 1982, JAMES et al. 1988a, 1996). In some cases, particularly for ponderosa pine (*Pinus ponderosa* LAWS.), seedcoats may remain attached to cotyledons for extended periods with contaminating fungi attacking cotyledons (JAMES 1992a, 2003a); these fungi can then move down the stem of young germinants causing mortality (JAMES 2003a).

Although *Fusarium* spp. are usually associated with root diseases, in some cases these fungi can cause either stem cankers or top blight of container seedlings (HANSEN et al. 1990, JAMES 2003a, b, JAMES et al. 1991). *Fusarium* sporodochia may be produced above the ground line of infected seedlings (JAMES 1985c, 1992a, 2005a). These produce spores that can readily be disseminated throughout greenhouses via air movements or during irrigation (JAMES 1984a, 2002b). Top blight occurs when susceptible seedlings are kept under very moist conditions and foliage does not readily dry out between irrigations (HANSEN et al. 1990, JAMES 1991a, 2002b). This type of disease can spread very rapidly and must be dealt with aggressively with sanitation and fungicides to preclude extensive losses.

By far, root diseases are the most important diseases of container-grown seedlings caused by *Fusarium*. Although an extremely wide variety of *Fusarium* spp. can be associated with root-diseased seedlings (JAMES et al. 1989), *F. proliferatum* (MATSUSHIMA) NIRENBERG is the most common and probably the most virulent species (JAMES 1997a, JAMES et al. 1997). This species is not commonly seedborne (JAMES 1997a, 1999), nor does it reside commonly either in nursery soil or peat-based growing media (JAMES 1985a, 2005b). Also, *F. proliferatum* does not form long-lived resting structures such as chlamydospores like several other *Fusarium* spp. found in forest nurseries (GERLACH, NIRENBERG 1982, JAMES 1997a, LESLIE 1991, NELSON et al. 1983). However, *F. proliferatum* successfully colonizes organic matter within or adjacent to greenhouses (JAMES 1983, 1984a) and, once established within greenhouses, can spread very rapidly because it produces long chains of microconidia which are readily disseminated via air movements (GERLACH, NIRENBERG 1982, JAMES 1997a, 2005a, NELSON et al. 1983). Seedling infection by this pathogen can occur early in the growth cycle, even though disease symptoms may not initially appear (JAMES 1985e, JAMES et al. 1987). In most cases, the fungus penetrates root epidermis and colonizes cortical cells, often without causing tissue necrosis (JAMES 2004b, JAMES, GILLIGAN 1988a). Disease symptoms often become more noticeable near the end to the growth cycle when seedlings are stress to stop growth (set buds) and harden off (JAMES 2000c, JAMES et al. 1987). At this time, seedling tip dieback and top necrosis becomes evident (JAMES 1987a, 1988c, 2002b, 2005a, JAMES et al. 1988b). Eventually, entire seedlings are killed. In some cases, seedling growth is severely limited by root infection with *F. proliferatum*, even though above-ground disease symptoms are not apparent (DUMROESE et al. 2002). When root disease is severe, losses can be extensive and may result in a large portion of the crop (JAMES 1997a, 2004b, JAMES, GILLIGAN 1984).

Host ranges

Although many different conifer species are affected by *Fusarium* spp. in containers, the most commonly affected species are Douglas-fir, ponderosa pine, western white pine (*Pinus monticola* DOUGL.), western larch (*Larix occidentalis* NUTT.) and lodgepole pine (*Pinus contorta* DOUGL.). All these species respond similarly to infection by *Fusarium*. However, in some cases, root decay of western white and whitebark (*Pinus albicaulis* ENGELM.) pine seedlings can be very extensive without above-ground symptoms becoming evident (JAMES 1985d, 1988a, 1991a, b, 2000b). In such cases, *Cylindrocarpon* spp. (especially *C. destructans* (ZINS.) SCHOLTEN) colonizes roots at high levels along with *Fusarium* spp. (JAMES 1983, 1991a, 1995, 2000b, JAMES, GILLIGAN 1986).

Douglas-fir grown in greenhouses is especially susceptible to *Fusarium*, particularly *F. proliferatum* (JAMES 1985e, 1986b, c, 2005a, JAMES et al. 1986, 1987, 1989, 1995a, 1997). At some nurseries, it is rare if the Douglas-fir crop is not adversely impacted by this pathogen. Unfortunately, by the time disease symptoms become evident, little can be done that effectively reduces losses. Fungicides are usually not effective near the end of the growth cycle (JAMES 1984b, 1988b, JAMES et al. 1991, SHRIMPTON, WILLIAMS 1989), probably because of extensive root colonization by *Fusarium* and limitations in distribution of chemicals in sufficient concentrations throughout root systems growing in containers.

Inoculum sources

As indicated previously, conifer seeds are important sources of *Fusarium* inoculum in container operations (JAMES 1984c, 1986a, b, 1987d, JAMES, GENZ 1982). Level of seed contamination varies widely throughout different seedlots (JAMES 1985c, 1999, 2004b, JAMES et al. 1996) and pathogens can spread extensively during stratification that is usually necessary prior to sowing (JAMES 1987d, 1999). We usually recommend that chemical seed treatments are necessary when level of *Fusarium* contamination exceeds about 10% of tested seeds, even though not all isolates are necessarily potential pathogens.

Another very important inoculum source is reused plastic or Styrofoam™ containers (JAMES 1990, 2001, JAMES, GILLIGAN 1988a, JAMES et al. 1988c). *Fusarium* is often present within or on the inner walls of containers. Inoculum occupies both roots of previous seedling crops and organic matter left after seedling extraction (JAMES 1992b, JAMES, EGGLESTON 1997, JAMES, SEARS 1990). We have found that most inoculum is concentrated near the bottom of container cells (JAMES 1989, 2001, JAMES, GILLIGAN 1988b, JAMES et al. 1988c), probably because conditions are more conducive there for pathogen survival and propagules may naturally move to the bottom of cells as irrigation water drains from the container or other effects of gravity.

Other important pathogen inoculum sources in container nurseries include organic matter residing inside greenhouses, on walls, floors, and benches (JAMES 1984a, 1988c, 2003a, JAMES et al. 1990, 1995b, SUTHERLAND, VAN EERDEN 1980). Some *Fusarium* spp. can probably remain viable for long periods on organic debris within greenhouses. These fungi can also colonize weeds growing within or adjacent to greenhouses (JAMES 1984a, JAMES et al. 1990).

Insects occurring within greenhouses may be important vectors of some fungal pathogens. For example, adult fungus gnats (Diptera: Sciaridae) were shown to carry *Fusarium* and other pathogens such as *Botrytis* (JAMES et al. 1994). It is likely that these fungi are passively carried by insects during their feeding on container seedlings.

We have not evaluated the potential of irrigation water to introduce *Fusarium* propagules into greenhouses. However, it is unlikely that these fungi are commonly spread in irrigation water, particularly when water comes from deep wells.

Peat-based growing media (containing either vermiculite, perlite, or sawdust) from commercial sources are usually not contaminated with *Fusarium* spp. (JAMES 1985b, JAMES et al. 1990).

Although such media are not sterile, in some cases, it is steam treated to reduce chances for pathogen contamination while maintaining populations of desirable organisms such as certain spore-forming bacteria. On rare occasions *Fusarium* contamination of growing media may occur and seriously impact seedling crops (JAMES 2005b, JAMES, GILLIGAN 1984).

Disease management

Management of *Fusarium* diseases in container seedling crops is most effective through conscientious efforts at prevention. The major goals of disease prevention are to reduce levels of pathogen inoculum within and adjacent to seedling growing environments (JAMES 2004b, JAMES et al. 1988a, 1990) and reduce stress levels on seedlings during production (JAMES 1984b, 1997b, 2004b, JAMES et al. 1990).

Pathogen inoculum can be effectively reduced from seeds, peat-based growing media, reused containers, and greenhouse environments. Seeds may be treated with chemical sterilants to reduce levels of seedcoat contamination by pathogenic fungi (DUMROESE et al. 1988, JAMES 1986a, 1987c, JAMES et al. 1996). The most commonly-used sterilants include bleach (aqueous sodium hypochlorite) (DUMROESE et al. 1988, JAMES, GENZ 1981, JAMES et al. 1995b, 1996, WENNY, DUMROESE 1987), hydrogen peroxide (JAMES 1986a, JAMES, GENZ 1981), and selected fungicides (JAMES, GENZ 1981, JAMES et al. 1996). Major disadvantages of chemical sterilants include potential problems of worker exposure and potential phytotoxic responses by seeds or young germinants (JAMES 1986a, 1988b, JAMES, GENZ 1981). These may be overcome by treating seeds with running water rinses (JAMES 1987b, JAMES et al. 1995b, 1996) or hot water (JAMES et al. 1988). Running water rinses are most effective if carried out for at least 48 hrs with treated seeds being periodically agitated (JAMES 1987b, JAMES et al. 1996). It may be important to treat seeds prior to stratification because of the possibility of pathogens spreading throughout seedlots during stratification (JAMES 1999). We have found that placing seeds in standing water for prolonged periods of time prior to sowing is a good way of spreading contaminating pathogens throughout seedlots (JAMES 1999, 2004b, JAMES, GENZ 1981).

Plastic and Styrofoam containers are usually reused to grow several crops of seedlings. These reused containers can become contaminated with potential *Fusarium* pathogens that can infect and cause disease on subsequent seedling crops (JAMES, GILLIGAN 1988b, 1988c, JAMES et al. 1988c). Therefore, growers treat containers to reduce chances of pathogen carryover. High-temperature steam cleaning was previously the major way containers were treated (PETERSON 1990), but although most organic matter was removed from steam-treated containers, propagules of potential pathogens often remained (JAMES et al. 1988c). To deal with this, more effective treatments were needed. Chemical sterilants, such as sodium metabisulfite (DUMROESE et al. 1993b, PETERSON 1990), aqueous bleach solutions (JAMES, SEARS 1990, PETERSON 1990), and copper solutions (DUMROESE et al. 2002) were evaluated. However, problems of worker exposure and disposal of toxic chemicals led to seeking alternative treatment methods that were more innocuous. Immersion in hot water (80 °C for 30 seconds for styrofoam and 66 °C for 15 seconds for plastic containers) was found to be effective (JAMES 1992b, JAMES, EGGLESTON 1997, JAMES, WOOLLEN 1989, JAMES et al. 1990). However, hot water immersion can be expensive due to high energy costs required to maintain high temperatures for prolonged periods. Therefore, other treatments, including radio frequency waves (JAMES, TRENT 2001), dry heat (JAMES, TRENT 2002), and large-room steam treatment (TRENT et al. 2005) were tested and performed comparably with standard hot water immersion.

We have periodically attempted biological control of *Fusarium*-associated diseases. Our choices of test biocontrol agents were limited by those that were commercially available, which were developed from other agricultural cropping systems. As a result, our results were not good as we had hoped. Examples of the organisms we have previously tested included *Streptomyces gris-*

eoviridis L. ANDERSON (DUMROESE et al. 1998), *Gliocladium virens* MILLER, GIDDENS & FOSTER (DUMROESE et al. 1996), *Trichoderma harzianum* RIFAI (JAMES 2000a, MOUSSEAUX et al. 1998) and a non-pathogenic strain of *F. oxysporum* (JAMES 2002a). Most of these tests have occurred under tightly controlled laboratory or greenhouse conditions. In general, the tested organisms may have reduced populations of potential *Fusarium* on roots of tested conifer seedlings, but usually not to levels possible with chemical pesticides. Effects on disease levels varied among the tested biocontrol organisms; significant differences between treated and non-treated seedlings were often not found. We suspect that potential biocontrol agents specifically adapted to forest nursery environments would perform more satisfactorily. For example, we believe that specific strains of non-pathogenic *F. oxysporum* obtained from forest nurseries should provide viable biological control of other *Fusarium* spp., particularly pathogenic *F. oxysporum* and *F. proliferatum*.

Outplanting performance

Because of high levels of root colonization by potentially-pathogenic *Fusarium* spp. on seedlings produced in nurseries, forest managers and nursery growers were concerned about possible impacts of this colonization once seedlings were outplanted on forest sites. We have periodically seen high levels of seedling mortality and poor growth of surviving seedlings following outplanting (JAMES 1988a, 1991b). Although *Fusarium* spp. were commonly found on roots of poorly-performing seedlings and could readily be isolated from seedlings during cold storage (JAMES 2003c), their actual role in seedling deterioration was unknown. Therefore, we monitored seedling performance and root colonization by *Fusarium* spp. following outplanting over time (DUMROESE et al. 1993a). Our results were similar to previous work (SMITH 1967) that showed that *Fusarium* obtained when seedlings are grown in nurseries is gradually replaced by other mycoflora following planting in forest soils. Mortality that might have occurred following planting is usually not related to *Fusarium* on root systems. Environmental conditions, particularly moisture, and animal damage are the most important factors affecting seedling performance following outplanting.

Pathogenicity testing

During the course of our investigations, many different *Fusarium* spp. were isolated from diseased seedlings, containers, and seeds. We expected that some of these species would likely be more virulent on nursery crops than others. In order to test this hypothesis, we developed techniques that could be used to relatively quickly ascertain potential of selected *Fusarium* isolates to elicit disease under both laboratory (JAMES 1996, JAMES et al. 1986, MILES, WILCOXSIN 1984) and greenhouse (JAMES et al. 1989, MILES, WILCOXSIN 1984, MOUSSEAUX et al. 1998) conditions.

In general, we found that isolates of *F. oxysporum* varied widely in their levels of virulence on young, conifer seedlings (JAMES et al. 2000). However, most tested isolates of *F. proliferatum* exhibited capacities to be very aggressive pathogens (JAMES et al. 1995a, 1997). Similar tests found that isolates of *F. sporotrichioides* SHERB., *F. acuminatum* ELL. & EV., *F. solani* (MART.) APPEL & WOLLENW., *F. culmorum* (W. G. SMITH) SACC. and *F. anthophilum* (A. BRAUN) WOLLENW., all of which were isolated from diseased conifer seedlings, had much less virulence potential than either *F. oxysporum* or *F. proliferatum* (JAMES 2000c, 2004a, b, JAMES, PEREZ 1999, 2000). We concluded that these other *Fusarium* spp. were mostly saprophytes, at least under the conditions of our tests.

MOLECULAR CHARACTERIZATION OF *FUSARIUM OXYSPORUM*

As indicated previously, we have had serious difficulties interpreting the role of many *Fusarium* isolates we find in nurseries in their ability to elicit disease symptoms. Many of the potential pathogens we have studied are within the *F. oxysporum* species complex. This group of organisms,

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although appearing morphologically similar, displays wide genetic variability (GORDON, MARTYN 1997, KISTLER 1997). Some of this genetic variation may be related to pathogenic potential of selected hosts (GORDON, MARTYN 1997, JAMES 2004b). Therefore, studies were initiated to quantify genetic population variability and determine if genetic markers were available that could be used to differentiate pathogenic from nonpathogenic isolates of *F. oxysporum* from forest nurseries. Early results of this work indicate that specific genetic markers for pathogenic strains occur (DONALDSON et al. 1995, STEWART et al. 2004, 2005b) and it is possible that these may be used to develop molecular probes that could be used for early detection of pathogens in plant tissues and quantification of pathogen populations in nursery soil (STEWART et al. 2005a, b). If such probes can be developed and become available, they will greatly enhance our abilities to predict disease severity before it occurs so that adequate preventative measures can be taken by nursery growers.

CONCLUSIONS

Fusarium spp. are probably the most important group of pathogens causing diseases of seedlings in western North American forest nurseries. Although several different species may be involved, the two most commonly encountered are *F. oxysporum* and *F. proliferatum*. The former is more important as a pathogen of bareroot seedlings, while the latter is most important on container seedlings. Both species are common root endophytes and are capable of becoming pathogenic under certain environmental conditions. *Fusarium* spp. can be introduced into nursery crops via contaminated seeds, container growing media, reused Styrofoam or plastic containers, nursery soil, non-crop plants within or near nurseries, and from dormant propagules occurring on previous seedling crops. The best approach in reducing disease losses due to *Fusarium* spp. is prevention, primarily by reducing potential pathogen inoculum. This can be done by seed, container, growing media, and soil treatments to eliminate or reduce inoculum. In addition, cultural manipulations during crop growth cycles can help reduce seedling stress and abilities of potential pathogens to elicit disease. Biological control shows promise by introducing organisms that compete with or antagonistic toward pathogens. New research using techniques of molecular biology show promise in improving our abilities to detect and manage important *Fusarium* pathogens in forest nurseries.

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