Phytophthora root disease and the need for clean nursery stock in urban forests: Part 2 *Phytophthora* and nurseries

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ALTHOUGH INTRODUCED *Phytophthora* species have long been recognized as important pathogens in agriculture and urban forests (Erwin and Ribeiro 1995), the impacts of these pathogens in urban forests are often overlooked. Plants with Phytophthora root rots will underperform compared to non-infected plants. Plants may fail to establish, grow very slowly, be more prone to water stress, and die prematurely. However, without specific testing to check for the presence of *Phytophthora* in affected plants, such symptoms are commonly attributed to other causes.

Infected nursery stock has been identified as a high-risk pathway through which *Phytophthora* pathogens are moved into both cultivated and native habitats (Baker 1957, Bienapfl and Balci 2014, Bourret et al. 2016, Ferguson and Jeffers 1999, Jung et al. 2015, Parke et al. 2014, Rooney-Latham et al. 2015, Rooney-Latham et al. 2018, Schwingle et al. 2007, Sims et al. 2018, Yakabe et al. 2009, Zentmyer et al. 1952). Because *Phytophthora* species have been common in nursery stock for many decades, these pathogens have been introduced into many landscapes where infected nursery stock has been planted. Increased international trade in live plants in recent years has increased the diversity of *Phytophthora* species in both nursery stock and landscape plantings, increasing the potential for new disease problems.

This article is the second in a three-part series. In the first part of this series (Swiecki et al. 2018), we described how Phytophthora root rots have become more common in diverse landscapes and the risk they pose to landscapes. Because many *Phytophthora* introductions result from planting infected nursery stock, in this article we explain why Phytophthora root rot occurs so commonly in conventionally-produced nursery stock. In Part 3 of this series, we will discuss how to break the cycle of Phytophthora root rot in nurseries by integrating phytosanitary practices into all phases of nursery plant production. By using this clean production system approach, nursery stock can be produced that is free of *Phytophthora*. We will also discuss options for managing landscapes already affected by root-rotting *Phytophthora* species.

> *… disease development requires a favorable alignment of three factors: a susceptible host plant, a virulent pathogen, and a conducive environment.*

The plant disease pyramid

To understand why *Phytophthora* species are so common in nurseries, we need to consider the factors that influence the *Phytophthora* disease cycle that was described in Part 1 of this series (Swiecki et al. 2018). The development of plant diseases is commonly described through a simple conceptual model known as the plant disease triangle. This simplified model shows that disease development requires a favorable alignment of three factors: a susceptible host plant, a virulent pathogen, and a conducive environment. A key concept conveyed by the plant disease triangle is that removing any part of the triangle – suitable host, pathogen, or environment – will prevent disease from developing.

A more complete model of plant disease development can be developed by dividing the environment into biotic agents (such as other interacting microorganisms) and abiotic or physical factors (such as temperature and moisture) and adding the element of time (**Fig. 1**). Variations of this expanded model are known as the plant disease pyramid. For many diseases, especially those caused by soil-borne pathogens, the activity of other microorganisms may favor or inhibit pathogen activity. These may include microorganisms in the rhizosphere (the zone of soil surrounding plant roots that is influenced by root processes and products) as well as those that colonize the root surface (rhizoplane) or grow within plant roots (such as mycorrhizal fungi). The biotic environment interacts with both the pathogen and the host and is influenced by abiotic environ-

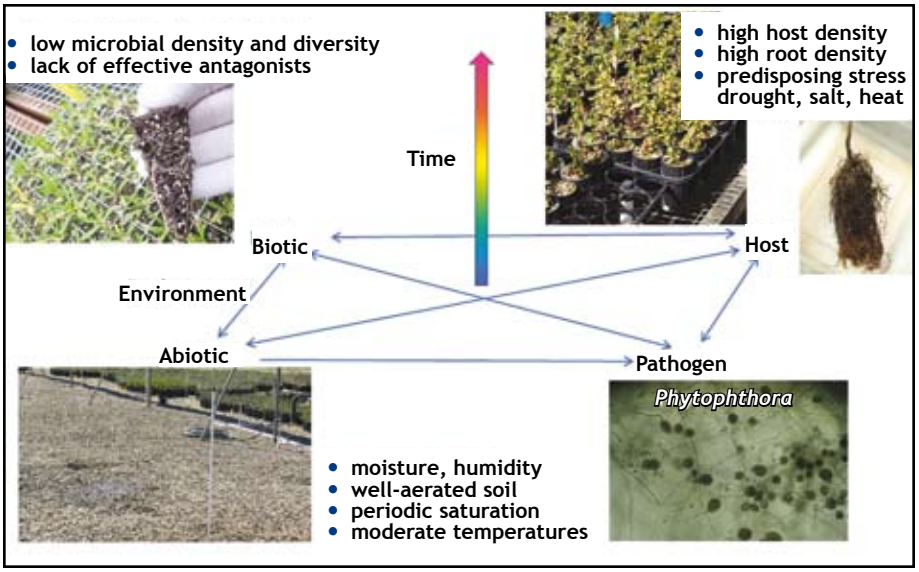
mental factors such as temperature and moisture.

The interactions between host, pathogen, and abiotic and biotic environment all occur through the dimension of time (**Fig. 1**). The time requirements for infection, growth, reproduction, and dispersal of the pathogen are influenced by environmental factors such as temperature and moisture. These factors vary depending on the host and pathogen. Disease development is inhibited if the conditions that favor disease do not persist long enough.

This model provides a framework for predicting conditions that will favor or impede infection and disease development. For instance, resistance or susceptibility to a given pathogen strongly affects the disease outcome for a given host. However, environmental stresses, including water deficit and salinity, can alter host resistance levels, predisposing stressed plants to greater disease severity (Boyer 1995, DiLeo et al. 2010, Erwin and Ribeiro 1996, MacDonald 1982, Swiecki and MacDonald 1988, 1991). As another example, the reproduction of root-rotting *Phytophthora* species is strongly influenced by the density of susceptible host roots. High root density favors disease spread through an individual plant's root system and across a population of plants. Root density and distribution are shaped by the interaction between the plant and its environment and thus can vary within and between sites because of soil conditions, irrigation patterns, or other factors.

Because of these complex interactions, different disease outcomes may develop for a given host-pathogen combination and disease can progress at different rates under different conditions. Root-infecting *Phytophthora* species may function as fine root nibblers, lethal crown rot pathogens, and many variants between these extremes. As a result, symptoms for a given host-pathogen interaction may range from a lack of obvious symptoms, to stunting, various levels of dieback, slow decline, or rapid plant collapse. This range in symptom expression complicates disease diagnosis and adds considerable uncertainty to predicting disease trajectories and impacts.

Figure 1. Diagram of the plant disease pyramid, showing interactions between various factors that affect the development of Phytophthora root rot in nurseries. Disease will not develop if any of the factors at the base of the pyramid absolutely limit disease (e.g., resistant host, lack of pathogen, highly antagonistic microbial environment, unsuitable temperature and moisture) or if favorable conditions do not persist long enough. Reciprocal interactions exist between factors (blue arrows). For example, host plants are affected by the abiotic environment (e.g., high temperature, low soil moisture can induce water stress) and the local abiotic environment can be affected by host plant (e.g., plant canopy can reduce soil temperature, increase humidity). The main exception is that *Phytophthora* generally has little direct effect on the abiotic environment.



Nurseries are very favorable for *Phytophthora* disease development

If we consider the factors in the plant disease pyramid (**Fig. 1**) along with the features of the *Phytophthora* disease cycle (see Swiecki et al. 2018), it becomes clear how nurseries provide nearly optimal environments for the development and spread of *Phytophthora* diseases (Junker et al. 2016, Leonberger et al. 2013, MacDonald et al. 1994, Parke et al. 2014).

Pathogen factors: *Phytophthora* can contaminate plants in a nursery through many routes. These can include use of infested potting media; use of contaminated irrigation water from untreated surface water sources; transfer of infested soil via dirty containers, tools, and hands; or placing containers on the ground where they are exposed to spores in water puddles or contaminated soil (**Fig. 2**). Once *Phytophthora* species are present in a nursery, they can reproduce rapidly and abundantly on susceptible host roots and spread between containers via water splash and incidental movement of soil and debris.

Host factors: Compared to a plant growing in native soil, a plant grown in a nursery has a much denser root system, which is concentrated in a small volume. Along with close interplant spacing in nurseries, the density and distribution of host roots provides nearly optimum conditions for *Phytophthora* reproduction and spread. Nursery plants are com-

monly grown in blocks that contain a single species or clonal variety, so host susceptibility is quite uniform within the blocks. Handling and moving containers increase opportunities for pathogen spread. The small rooting volume in containers can lead to frequent stresses to the roots: water deficits, excessive heating, and a buildup of salts from fertilizers and irrigation water with elevated salinity. As noted above, these predisposing stresses can make plants more susceptible to *Phytophthora* infection.

Abiotic environment: Environmental conditions in nurseries are typically quite favorable for *Phytophthora*. Temperatures in nurseries are commonly maintained in a moderate range suitable for plant growth and favorable for many *Phytophthora* species. Nursery plants need to be irrigated frequently, resulting in both regular periods of soil saturation and an environment that is generally moist and humid, though subject to fluctuating moisture levels that can cause periodic host stress. Even if the potting medium drains quickly, the lower portion of the container normally remains saturated for an extended period. These conditions provide ample moisture for sporangium production and the release and dispersal of zoospores. Potting media is normally well-aerated, which also favors sporangium production. Large pore spaces typically found in potting media also facilitate zoospore movement within containers. High porosity also allows zoospores to leach out of containers and be dispersed in runoff and splash.

Biotic environment: Soils that suppress *Phytophthora* root diseases are characterized by high densities of antagonistic soil microorganisms. The media in nursery containers are simplified systems that typically lack the density and diversity of microorganisms needed to strongly suppress *Phytophthora.*

Time: Favorable conditions for infection and disease development commonly persist as long as plants are maintained in the nursery. Plants grown in the nursery for extended periods have more chances of becoming infected via splash or runoff from other infected plants. Hence, larger stock that has been held in the nursery for a longer period has a higher likelihood of being infected.

For practical and economic reasons, container nurseries are designed to grow as many plants as possible in the smallest possible amount of space. As an unintended consequence, nurseries are also highly favorable for the development and spread of *Phytophthora* root diseases as well as other plant diseases. The nature of high-density nursery production does not allow host or environmental factors to be altered enough to prevent *Phytophthora* root diseases. Hence exclusion of the pathogen provides the only viable option for producing nursery plants that are free of *Phytophthora*. If the pathogen is not present, disease will not develop even if host and environmental conditions favor disease development.

Unfortunately, few nurseries have implemented the comprehensive set of management practices needed to exclude *Phytophthora*. Instead, common production practices provide many opportunities for contaminating nursery stock with *Phytophthora*. These practices include:

- use of nonpasteurized potting media, sometimes including the reuse of media from diseased plants;
- reuse of dirty containers, including those obtained from sources outside of the nursery;
- placing containers on the ground, which serves as a reservoir for *Phytophthora* (Parke et al. 2014);
- bringing infected plants from other sources into the nursery; infected plants may lack obvious symptoms (Beinapfl and Balci 2014, Migliorini et al. 2015);
- using systemic fungicides that suppress *Phytophthora* symptoms but do not eliminate the pathogen (Rupp et al. 2016).

This last factor, risks from use of systemic oomycete fungicides, may seem counterintuitive and is discussed in detail below.

Figure 2. High root density and close interplant spacing in nurseries provide nearly optimum conditions for disease spread and pathogen reproduction. Placing containers on the ground exposes plants to inoculum in water puddles or contaminated soil.

Fungicide use in nursery stock as a disease risk factor

Because nurseries are so conducive to *Phytophthora* diseases, many nurseries routinely use systemic chemicals to suppress *Phytophthora*. These

chemicals are commonly known as fungicides, though this term is both inaccurate and misleading in this context. *Phytophthora* is a member of the water molds (also known as Oomycota or oomycetes), which are only distantly related to true fungi. Furthermore, these systemic chemicals may suppress disease but do not actually kill *Phytophthora* in soil or infected plant tissues when used at label rates. Hence, these materials are more correctly called systemic oomycete suppressive (SOS) chemicals rather than fungicides. Although SOS chemicals can decrease economic losses caused by *Phytophthora*, their use has not stopped the proliferation of *Phytophthora* in nurseries. (Yakabe et al. 2009, Beinapfl and Balci 2014, Parke et al. 2014, Jung et al. 2015, Beaulieu 2015).

SOS chemicals (systemic "fungicides") with strong inhibitory activity against water molds have become widely used to control Phytophthora root and crown rot since they were first introduced in the late 1970s. One widely used class of these chemicals, the phenylamides, includes metalaxyl (Subdue®) and mefenoxam (Subdue Maxx®, one of the two optical isomers present in metalaxyl). Phenylamides primarily protect against infection and can move both upward and downward in plants. They do not affect zoospore release, germination, or penetration, but rapidly inhibit further development in infected hosts. They inhibit ribosomal RNA synthesis by specific interference with activity of a nuclear RNA-polymerase - template complex. This single-site activity poses a risk for the development of fungicide resistance and resistance to phenylamides has been reported for a number of *Phytophthora* species (Hu et al. 2008, Hwang and Benson 2005). Phenylamides have fairly long residual activity, generally 70-90 days.

Phosphonates are a very different class of systemics with activity against oomycetes. They include potassium phosphite and other salts of phosphorous acid (e.g., Agri-Fos®, Reliant®) as well as fosetyl aluminum (Aliette®), which is converted to phosphite ion (PO_3^{-3}) within plants. Phosphite (=phosphonate) is highly systemic, translocating both upward and downward in plants. Plants cannot utilize phosphite as a source of phosphorous. Nonetheless, it tends to accumulate at phosphorus sinks within plants, including developing fruits and roots. Phosphite primarily has protectant activity and reduces, but does not prevent, zoospore production in infected plants (Wilkinson et al. 2001). At high concentrations in the plant, phosphite is directly toxic to *Phytophthora* species. At lower concentrations, phosphite acts indirectly by increasing a plant's natural resistance response to *Phytophthora* infection (Guest and Grant 1991, Hardy et al. 2001). At these lower concentrations, phosphite has sublethal effects on *Phytophthora* metabolism, which cause the pathogen to release compounds that trigger host defense responses. Residual activity of phosphite can be two years or more in field-grown plants (Shearer and Fairman 2007, Swiecki and Bernhardt 2016).

Many other SOS chemicals are registered for use against *Phytophthora* diseases, and research to identify new chemicals is ongoing. Depending on the chemical group, these chemicals differ with respect to many properties, including:

- biochemical mode of action;
- level of activity against different *Phytophthora* species;
- life stages of the pathogen that may be inhibited;
- degree of systemic movement within plants;
- residual activity and environmental fate;
- toxicity to nontarget organisms;
- potential for resistance development.

It is critical to remember that these SOS chemicals suppress but do not eliminate *Phytophthora* infections (Shishkoff 2014). Even SOS chemicals that show "eradicative" (post-infection) activity within plants (e.g., phenylamides) will not affect *Phytophthora* oospores or chlamydospores in dead and dying roots because these chemicals are not translocated into dead tissues. Likewise, resistant *Phytophthora* propagules dispersed into the soil or potting mix that serve as a reservoir of inoculum to initiate new infections are not usually affected by these chemicals.

The effects of SOS chemicals are strongest when the chemicals are present at optimum concentrations in the treated plants. However, in both field settings and container nurseries, it is difficult to consistently apply chemicals uniformly to all plants, especially where plant canopies overlap. Treated plants commonly receive varied doses, some too low to be effective. Although SOS chemicals are systemic, concentrations vary within the plant and between older and younger tissues, so some roots in a treated plant may not have effective levels of these suppressive chemicals. Furthermore, these chemicals have much less effect on plants with existing infections than on uninfected plants. Also, if *Phytophthora* strains have developed resistance to the SOS chemical being used, the chemical will provide little or no disease suppression.

As a result of these limitations, plants treated with SOS chemicals, including more recent materials such as isoxazolines (e.g., oxathiapiprolin = Segovis®, Zorvec®), can still become infected by *Phytophthora* (Benson 1987, Hamm et al. 1984, Ji et al. 2014, Matheron and Porchas 2015, Rupp et al. 2016, Tjosvold et al. 2008). If levels of SOS chemicals are high enough in the host tissue, subsequent pathogen growth and reproduction will be suppressed. This can reduce disease cycling and symptom development but does not eradicate the pathogen from the treated plant. When chemical residues in tissues decline, pathogen activity can resume. In short, a *Phytophthora*-infected plant treated with SOS chemicals remains infected, even if root rot symptoms are reduced.

Consequences of relying on chemical disease suppression in nurseries

Using SOS chemicals to suppress *Phytophthora* root disease can be a viable management strategy for field-grown agricultural crops and landscapes. By suppressing new infections and slowing disease progress in infected plants, yields can be improved compared to untreated plants and plant survival can be extended. In nurseries producing plants for planting, SOS chemicals also serve to suppress symptom development in infected plants, reduce losses due to mortality, and increase the output of saleable plants. However, even when SOS chemicals are used, disease cycling is not completely inhibited. *Phytophthora* infections can continue to spread among treated plants, especially under nursery conditions that strongly favor disease development.

Using SOS chemicals to suppress *Phytophthora* diseases in nurseries can result in the production of infected but largely asymptomatic plants (Shishkoff 2014).

Purchasers of cryptically-infected stock are buying a product with a concealed defect. (Migliorini et al. 2015) As the levels of SOS chemicals in the plants decline after planting, *Phytophthora* activity can increase if conditions are favorable. This can eventually result in the decline and death of the infected plant, though obvious symptom development may be delayed for months to years after planting. With this delay, people often overlook the connection between the dead or dying plant and the original, cryptically infected nursery stock.

While poor plant performance and early mortality are clearly undesirable, the situation is exacerbated by the fact that *Phytophthora*-infected plants can infest the planting site. Even if the infected plant is removed, the pathogen can remain behind in dead root fragments and resistant spores, which are in position to infect the next planting. Replanting with infected stock may also introduce additional *Phytophthora* species to the planting site. Because *Phytophthora* host ranges vary widely, the effective host range of a mixed *Phytophthora* infestation is usually wider than that of any single species. If a site has a mixed *Phytophthora* infestation, the list of species that may tolerate or resist infection will become shorter, limiting the likelihood of success for future plantings.

Roots of adjacent susceptible host plants, either natural vegetation or planted stock, that extend into the infested soil can also become infected, accelerating the rate at which the *Phytophthora*-infested area expands over time. Infested areas can also serve as a source of pathogen propagules that can spread via water runoff or be transported in soil and plant debris to other areas with planted or native vegetation. Over time, these processes can spread *Phytophthora* widely through a landscape.

Figure 3. *Phytophthora* was detected from the six maple trees in the two center columns (marked by yellow lines on rims in front row) of 15-gallon containers, which exhibited no obvious top symptoms. *Phytophthora* spores were detected in the group of trees by baiting irrigation leachate with green pear fruit. In close-packed arrays such as this, irrigation or rainstorms can splash infested soil and spores from one container to another.

Difficulty of detecting diseased nursery plants

For many pests and pathogens that affect leaves and stems, visual inspections can be effective for identifying affected plants or groups of plants, so careful inspections can be used to reject affected plants. Unfortunately, visual inspections are largely ineffective for detecting Phytophthora root rots (Osterbauer et al. 2014). Infection occurs long before visible symptoms develop aboveground, so diseased plants may not show visible symptoms (**Fig. 3**). For example, Standish et al. (1982) showed that in nursery-grown *Juniperus* spp., foliar symptoms only became apparent when over 50% of the root systems were decayed by *P. cinnamomi*. We have observed that many Californian drought-tolerant native species (e.g., toyon, *Heteromeles arbutifolia*) growing under nursery conditions do not show obvious top symptoms even when nearly all their roots are decayed (**Fig. 4**).

Careful root inspection can identify some infected plants at earlier stages, but examining roots is difficult, time consuming and can be destructive. At early disease stages, many healthy-appearing roots will be present, and it may be necessary to pull apart or wash out the entire rootball to find symptomatic roots. In many woody species, healthy roots and diseased roots may not show clear differences in color or appearance. Due to a variety of factors, it can also be difficult to distinguish between root turnover caused by abiotic issues (such as excessive heat or episodic drought stress) and Phytophthora root rot. Hence, even careful, thorough visual root inspections will likely not identify all infected plants. Furthermore, dislodging soil and roots while removing plants from pots can inadvertently spread contamination unless plants are handled carefully according to phytosanitary protocols.

As noted above, use of SOS chemicals may mask infected plants by reducing symptom development and expression (Shishkoff 2014). To overcome this, a common recommendation is to hold plants for 6 to 8 weeks after an SOS chemical application prior to inspection. This can help to reduce symptom masking, but the residual activity of some chemicals can be much longer than 8 weeks, especially if plants have been treated with high chemical rates. Furthermore, the resumption of Phytophthora root rot in woody plants commonly does not spike as soon as chemical residues decline. More commonly, disease activity increases gradually over many weeks or months as the residues drop and increasing numbers of roots become infected.

If inspection alone is inadequate, why don't we simply test nursery stock to determine if it is infected with *Phytophthora*? Various assays can be used to detect and identify *Phytophthora* species associated with nursery plants. These tests vary in difficulty, cost, sensitivity, and suitability for particular applications. However, caution is warranted because all testing methods can yield false negative results, i.e., *Phytophthora* is not detected when it is present. False negative results may arise for many reasons. All testing methodologies (e.g., immunoassay [ELISA], culturing, baiting, DNA-based methods) have limits in sensitivity and are subject to factors that can interfere with the tests. The quality, quantity, size, and condition of the sample, as well as the sampler's skill and experience level, can affect whether a pathogen is detected in a sample. False negative results may be obtained due to any of the following reasons:

- sample size is too small to capture detectable levels of the pathogen for the test being used;
- the amount of infection in the sampled plants is below detectible levels, e.g., because plants were recently infected;
- sampled plant(s) or roots are not infected, even though other nearby roots or plants are infected;
- infected roots are decayed by secondary organisms that interfere with detection of *Phytophthora*;
- *Phytophthora* species present does not infect baits being used or does not grow well on media used;
- pathogen growth is suppressed by SOS chemicals applied to the plant or potting soil;
- improper sample handling has degraded the pathogen to undetectable levels;
- the diagnostic test is run incorrectly or under conditions that reduce its efficacy.

Figure 4. Toyons (*Heteromeles arbutifolia*) in 1-gallon containers and their corresponding root systems. The leftmost plant was somewhat stunted, off-color, and appeared water-stressed, but did not have any dieback or leaf necrosis. It had extensive root rot. The center plant's top appeared healthy and some apparently healthy roots were seen on the outside of the root ball (center middle), but most of the remaining roots were rotted (center bottom). The plant at right was tall and its top looked healthy but nearly all roots were rotted. All three plants were infected with *Phytophthora cactorum*, which has a wide host range, including many species in the Rosaceae family.

Due to logistical, cost, and test sensitivity issues, it is impractical to individually test large numbers of plants to assess the infection status of each plant. To obtain a reliable supply of *Phytophthora*-free nursery stock, the plants needs to be produced under conditions that exclude *Phytophthora*. This is analogous to the way that the food service industry prepares food that is safe for consumption. Food safety relies on a system of clean handling and standardized safe preparation processes rather than testing every serving that is produced.

Effective testing still plays a role in monitoring the success of clean production processes. This will be discussed in Part 3 of this series, in which we describe how it is possible to produce nursery plants that are free of *Phytophthora* to the greatest degree practical.

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