

Soil Environmental Factors and Their Relationship to Avocado Root Rot

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Introduction

Factors that affect avocado root rot are complex and often interrelated, because they affect both the host avocado and root pathogen, *Phytophthora cinnamomi*. Some factors may affect the avocado negatively and the fungus positively, leading to a clear-cut increase in avocado root rot, while other factors may affect both the avocado and the fungus positively, leaving the resultant disease increase or decrease in root rot a matter of speculation. Furthermore, *P. cinnamomi* has several different life stages, such as zoospores, sporangia, and chlamydospores. Each stage of the fungus reacts differently to the external environment. For instance, drying the soil reduces zoospore survival but may increase sporangial production, so although the overall pathogen population decreases after drying the potential for long-term damage to avocado roots may increase. The following is a discussion of some of the soil environmental factors that affect avocado root rot and an attempt to understand the underlying reasons for these effects.

Soil Type and Drainage:

Soil with poor drainage, high clay content, high water tables, hard pans, clay pans, or areas where water pools after irrigation or rainfall have historically been associated with sites where avocado root rot is severe (Burns et al., 1980). Zentmyer and Ohr (1978) classified the soils in California according to their susceptibility to root rot. Soils with a severe hazard level have slow to very slow subsoil permeability, are poorly to very poorly drained, are less than 91 cm (36 inches) deep, and have clay textures. Soils with moderate hazard levels have a moderately slow permeability, are somewhat poorly drained, are 91 to 152 cm (36 to 60 inches) deep, and have clay loam textures. Soils with only a slight hazard for root rot development have a rapid to moderate subsoil permeability, are well drained, are over 152 cm (60 inches) deep, and have sand to loam textures. Poor drainage characteristics interact with the soil water to influence avocado root rot. It is unlikely that the rate of zoospore spread through soil is responsible for the increased root rot in clay soils. Zoospores of *Phytophthora* move in a helical spiral that requires a cylindrical space at least 190 μm in diameter to facilitate movement (Allen and Newhook, 1973). Heavy soils impede movement of zoospores, they travel three times further in coarse textured soil generally associated with low root rot hazard, than in clay soils (Duniway, 1976). However, zoospores will probably travel farther in surface flow on clay soils than on well-drained soils. It appears that any characteristics causing soil to maintain surface water or water-filled pores near the surface where avocado roots are concentrated for an extended period of time will exacerbate avocado root rot. Under these conditions, zoospores have an increased amount of time to be released and find their way to avocado roots through uninterrupted, water-filled channels.

Soil Moisture

Avocado root rot has been so closely associated with wet soils that before *P. cinnamomi* was discovered, the disease was known as melanorhiza and thought to be water injury (Horne, 1934). In reality, however, water really only favors the release and movement of *Phytophthora* zoospores. In most healthy avocado groves, the water in the surface soil ranges from 0 bar in matric potential after rain or irrigation to -1 bar as the soil dries out. Soils that remain wet or saturated become anaerobic (that is, lacking oxygen), and neither avocados nor *P. cinnamomi* will survive under those conditions. In poorly drained soils, water accumulates on the surface or is prevented from draining by impervious soil layers. Zoospores that are released only at matric potentials from 0 to -0.4 bar (Duniway, 1975) (Fig. 1) are easily spread from tree to tree in surface water or even through the soil (Kinal et al., 1993). The lengthy wet conditions provided by poorly drained soils will prolong the time the zoospores are able to swim through the pores in search of avocado roots. At lower water potentials of -0.25 to -1 bar, zoospores are actively restricted by air from swimming in the soil pores, and in addition, the diffusion of root exudates, which attracts the zoospores, is severely limited (Sterne, et al., 1977). Though very few sporangia are produced under saturated conditions, as the soil dries to matric potentials of -0.02 to -3 bar, sporangia are formed (Duniway, 1975). These sporangia usually await saturation in water before a new crop of zoospores is released. Mycelium can grow at 0 to -10 bar in the roots, and chlamydospores will readily form in this same range (Zentmyer, 1980). The chlamydospores, which are survival structures, are often stimulated to form by dry conditions, and they can survive for years under extremely dry conditions. Therefore, drying the soil will not rid it of *P. cinnamomi* (Fig. 1).

Improper water management can result in injury to the roots of avocado, which make them more susceptible to root rot. Flooding the soil for as few as three days can predispose the roots to heavy infection by *P. cinnamomi* by inducing the release of root exudates that attract zoospores (Kuan and Erwin, 1980). Drought stress can also injure roots and predispose them to avocado root rot during the next wet period (Duniway, 1977).

Soil Oxygen and Carbon Dioxide

Unfortunately, avocado is more sensitive to anaerobiosis than *P. cinnamomi*, and soil gas levels of 1% to 5% oxygen will damage or kill avocado roots (Stolzy et al., 1967). Air in well drained, aerated avocado soils may contain 15% oxygen and 0.03% carbon dioxide, while poorly drained soils may approach 1% oxygen and 16% carbon dioxide (Mitchell, 1970). These levels are achievable in soils with high organic matter and active respiring microorganisms. High carbon dioxide levels may play a role in the inhibition of *P. cinnamomi* by organic matter and in the formation of suppressive soils.

P. cinnamomi, like avocado, is an aerobic organism. It requires oxygen to grow and reproduce. Although periodically wet soils enhance *Phytophthora* populations, flooding will induce anaerobiosis and will result in a reduction of the soil *Phytophthora* populations (Stolzy et al., 1967). Zoospore release requires well-aerated irrigation water or rainwater containing 2.5% to 15% oxygen and 0% to 2% carbon dioxide (Fig. 1). Sporangial formation and chlamydospore germination require similar aerated conditions (Ioannou and Grogan, 1985; Mitchell, 1970). High levels of carbon dioxide are particularly inhibitory to sporangial formation and release. Interestingly, zoospore germination, hyphal growth in the infected root, and chlamydospore formation are not as restricted by oxygen and carbon dioxide levels and occur in the range of 0.1% to 15% oxygen and 0% to 20% carbon dioxide (Klotz, et al., 1963; Mitchell, 1970). In fact, it appears that low carbon dioxide levels (Ioannou and Grogan, 1985) stimulate chlamydospore production. It also appears that after dispersal in well aerated water, the fungus is capable of germinating, growing, and causing avocado root rot in poorly drained soils as the oxygen level decreases and the carbon dioxide levels increase (Stolzy et al., 1967). Mitchell (1970) believes that this may occur because the atmosphere in rotted roots is approximately 1% oxygen and 15% carbon dioxide (Fig. 1).

Under flooded conditions with low oxygen, chemicals such as hydrogen sulfide, nitrite, and ethylene may be generated. While these chemicals may significantly inhibit *P. cinnamomi*, they and the conditions under which they form are even more damaging to avocado roots (Zentmyer and Bingham, 1956).

Soil Nutrition

Bingham et al. (1958) reported that *P. cinnamomi* is incredibly adaptable and can survive and cause disease under a wide variety of soil chemical conditions. Specifically, they felt that variation in calcium, magnesium, potassium, and sodium levels in the soil would have little effect on avocado root rot. Zentmyer and Bingham (1956) found that nitrogen has no effect on avocado root rot as either the ammonium or nitrate form. Pegg et al. (1982), however, believe that nitrogen should be applied in the ammonium form and that nitrate may be conducive to avocado root rot. Others believe that minimal nitrogen applications should be made in root rot soil, because heavy applications of nitrogen of any kind may stimulate luxurious tree growth and therefore make the avocado more susceptible to root rot. *Phytophthora cinnamomi* can apparently damage avocado over a wide range of soil pH levels (3.5 to 8.0). Pegg (1983) proposes that growers should take advantage of the fact that high concentrations of cations such as K, NH₄, Ca, Mg, and Fe can induce encystment and reduce the viability of *P. cinnamomi* zoospores. He advocates the use of fertilizer, which is designed to induce maximum cations in the soil, supply nitrogen as ammonium or urea, and increase hydrogen ion excretion by the avocado root. Soluble cations in the soil are determined by soil chemistry, however, and are often difficult to sustain. In addition, microbial processes determine the amount of nitrate in the soil. Therefore, using fertilizer to reduce avocado root rot may prove difficult and requires further assessment. In general, it appears that altering nutrients does not greatly affect avocado root rot. There is, however, good evidence that organic matter, ammonia, and calcium can be inhibitory to avocado root rot.

Organic matter in the form of yard trimmings, avocado trimmings, corn stubble, sorghum stubble, wheat straw, alfalfa straw, and pine bark with a C:N ratio between 25:1 and 100:1 have been shown to be inhibitory to avocado root rot by many researchers (Borst, 1983; Broadbent and Baker, 1974; Downer, 1998; Pegg et al., 1982; Turney and Menge, 1994; Wolstenholme et al., 1996). Soils with organic matter content of 7% are thought to be inhibitory to *P. cinnamomi* (Turney and Menge, 1994). It has been suggested that organic material in soil can reduce avocado root rot by:

- 1) Increasing the activity of the indigenous micro-flora, resulting in suppression of the pathogen population through competition or specific inhibition (Broadbent and Baker, 1974);
- 2) Releasing degrading compounds such as carbon dioxide, ammonia, nitrites, or saponins or enzymes that are generally toxic to *P. cinnamomi* (Downer, 1998; Tsao and Oster, 1981);
- 3) Acting as a trap, since *Phytophthora* will be attracted to and encyst on organic matter (Grant et al., 1985);
- 4) Inducing plant defense mechanisms (Gilpatrick, 1969); and
- 5) Creating an environment that stimulates root development by physically inhibiting *Phytophthora* (Turney and Menge, 1994). Downer (1998) has shown that enzymes such as cellulase or glucanase are extremely disruptive to the life cycle of *P. cinnamomi* because its cell wall is composed of cellulose and glucans, unlike those of most other fungi. He found that organic matter has high concentrations of cellulases and glucanases due to the breakdown of cellulose and lignin compounds by microorganisms.

Applications of calcium as calcium carbonate, calcium nitrate, and calcium sulfate have also been shown to repeatedly reduce avocado root rot (Broadbent and Baker, 1974; Downer, 1998; Falcon et al., 1984; Halsall and Forrester, 1977; Lee and Zentmyer, 1982; Messenger-Routh, 1996; Pegg, 1983). Calcium may reduce avocado root rot by: 1) stimulating avocado root growth (Falcon et al., 1984); 2) increasing disease resistance in avocado roots (Lee and Zentmyer, 1982); 3) impairing the activity of *P. cinnamomi* by reducing sporangial formation (Halsall and Forrester, 1977); 4) interfering with zoospore motility (Donaldson and Deacon, 1993) or inducing premature encystment (Pegg, 1983); 5) improving soil drainage (Bakker et al., 1979); and 6) stimulating antagonistic microorganisms (Lee and Zentmyer, 1982). Messenger-Routh (1996) studied all of these mechanisms in California soils and determined that calcium primarily acted as a weak fungicide by reducing the size and number of sporangia produced by *P. cinnamomi*.

Ammonia gas, which may be released from organic matter, urea, or ammonium additions, has been shown to be very toxic to *P. cinnamomi* and can totally inhibit release of zoospores at concentrations as low as 0.16 ppm (Gilpatrick, 1969; Tsao and Oster, 1981; Tsao and Zentmyer, 1979). Unfortunately, this chemical is also toxic to avocado roots, and it is very difficult to manage this chemical in a way that is beneficial to avocados and toxic to *P. cinnamomi* (Gilpatrick, 1969; Tsao and Zentmyer, 1979). Nevertheless, the activity of this gas often explains many of the apparently anomalous findings associated with nitrogen and organic matter additions in avocado root rot situations.

Suppressive Soils

Much has been written about suppressive soils with respect to avocado root rot (Borst, 1983; Broadbent and Baker, 1974; Downer, 1998; Halsall, 1982; Ko and Shiroma, 1989; Pegg et al., 1982; Turner and Menge, 1994). Avocado root rot suppressive soils occur naturally. For example, natural rainforest habitats were suppressive to avocado root rot and a complex method called the Ashburner method was created to duplicate the suppressive rainforest soils (Broadbent and Baker, 1974). The Ashburner method consisted of cover cropping, applications of manure, dolomite, and superphosphate, and the addition of organic matter. Today the method has been modified to provide only the key ingredients, which are organic mulches and gypsum. High populations of bacteria and actinomycetes (Broadbent and Baker, 1974) or cellulose and lignin degraders (Downer, 1998) are naturally stimulated to create the suppressive soils. As we learn more about the factors that create suppressive soils, this term will lose its mystique and we will speak of specific suppressive factors. Certain bacteria, such as some species of *Pseudomonas* and *Chromobacterium violaceum*, are required to stimulate sporangial production of *P. cinnamomi*, while other bacteria are inhibitory (Erwin and Ribeiro, 1996; Zentmyer, 1980). Specifically, microorganisms such as *Myrothecium roridum*, *Trichoderma harzianum*, *Epicoccum purpurascens*, *Catenaria anguillae*, *Humicola fuscoatra*, *Anguillospora pseudolongissima*, *Hypochytrium catenoides*, *Myrothecium verucaria*, *Streptomyces griseoalbus*, *Micromonospora carbonacea*, *Streptomyces violascens*, and *Ceraceomyces tessulatus* have been shown to be inhibitory to *P. cinnamomi* via competition, antibiosis, or parasitism (Downer, 1998; Erwin and Ribeiro, 1996). The complex community structure of microorganisms like these is undoubtedly responsible for the fact that some soils are suppressive while others are not. Zentmyer (1980) draws attention to the fact that populations of *P. cinnamomi* usually drop off dramatically after the first wave of root rot occurs. He feels this may occur as parasites of *P. cinnamomi* and other antagonistic microorganisms invade and make the soil more suppressive.

Soil Temperature

Phytophthora cinnamomi is capable of growing under a wide range of temperatures from 9 to 33°C (48.2 - 91.4°F); however, activity is greatly reduced below 12°C (53.6°F) and above 30°C (86°F). By contrast, the avocado tree grows well between 21 and 33°C (69.8 - 91.4°F) but is inhibited below 21°C (69.8°F). Because the fungus grows better at cooler temperatures than does the avocado, root rot is often severe between 9 and 21°C (48.2 - 69.8°F). At temperatures between 28 and 33°C (82.4 - 91.4°F), the avocado tree appears to grow better than *P. cinnamomi* and root rot is reduced

(Zentmyer, 1980).

From the foregoing it is apparent that factors, which affect avocado root rot, are complex and often interrelated. Some factors may affect the avocado host negatively and the fungal pathogen positively, leading to a well defined increase in root rot, while other factors may affect both the host and pathogen positively, leaving the resultant increase or reduction in disease a matter of speculation. Considering all of the above it can be concluded that the observance of sound cultural practices (which include judicious irrigation and soil amendment with calcium and organic matter) and selection of suitable planting sites are a prerequisite to controlling avocado root rot caused by *Phytophthora cinnamomi*.

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Figure Legends

Figure 1. The relationship between soil matric potential and soil carbon dioxide (CO₂) and oxygen (O₂) levels, and the varying life stages of *Phytophthora cinnamomi* Rands.

