ROLE OF ENVIRONMENTAL STRESS IN THE DEVELOPMENT OF PHYTOPHTHORA ROOT ROTS[1]

by J.D. MacDonald

Phytophthora root rots are an important group of diseases affecting many woody and herbaceous plants. Some of these diseases are of great economic importance and are not always effectively controlled by fungicides, especially when they occur on trees in forest, orchard, or landscape plantings. The difficulties encountered in control have resulted in considerable research over the past 10-15 years to more precisely define conditions which favor production, survival and spread of inoculum of *Phytophthora* spp. in soil, and infection of plant roots. Such information eventually should provide a basis for development of effective cultural practices to aid in control of these diseases.

While greatly increasing our understanding of the effects of the environment on several species of *Phytophthora* (8), recent experiments also have shown that certain environmental extremes, which are stressful to plants, can markedly influence the occurrence or severity of Phytophthora root rots. This concept is not new in plant pathology, as environmental stresses are known to play a determining role in several diseases (5, 18, 19). However, these experiments are significant because they represent the first unambiguous evidence that stresses which are sometimes encountered by plant roots can significantly increase their susceptibility to diseases caused by *Phytophthora* spp. A complete knowledge of the forms and limits of stress which can be tolerated by plants without altering their susceptibility to Phytophthora root rots is important for the development of effective cultural controls and identification and deployment of stable genetic resistance. The purpose of this paper is to review some of the recent, well-documented examples which show that stress can increase the occurrence or severity of Phytophthora root rots and to discuss current hypotheses regarding mechanisms of action. Insofar as possible, work with woody plant species will be emphasized.

Flooding Stress

Conditions of high soil moisture are known to favor Phytophthora root rots and many reports in the literature substantiate this association. For example, early experiments by Wager (22) showed that a serious decline of avocados in southern California, which had been associated with excess water and variously termed water injury, melanorhiza, asphyxiation, or apoplexy, was actually a root disease caused by *P. cinnamomi.* He found that 2-3-year-old trees were not sensitive to flooding per se, as plants grown in soil in the absence of *P. cinnamomi* could be subjected to up to 9 days of continuous flooding with no apparent ill effects. However, if the soil was infested with *P. cinnamomi,* flooding for as little as two days could result in severe root rot. More recently, three species of *Phytophthora* were found to cause trunk cankers on coast live oak and cork oak trees in California, where they had been planted in areas of poorly-drained soil subject to periodic, prolonged water-saturation (15). Also Phytophthora root and crown rot of cherry trees was observed to be particularly severe in California following unusually heavy rainfalls during the winter of 1973-74 (16). In a follow-up study using methods to precisely control soil moisture, Wilcox and Mircetich (23) found that periods of soil saturation lasting 48 hr were required for development of severe root rot on mahaleb cherry rootstocks.

Historically, the occurrence of Phytophthora root rots in flooded soils has been attributed to requirements of the pathogen for high soil moisture (25). Indeed, evidence exists which indicates that soil-water status can exert a determining influence on several epidemiologically-important stages in the life of *Phytophthora* spp. Members of this

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genus reproduce by formation of sporangia which, under proper conditions, germinate to release free-swimming zoospores. The zoospores of *Phytophthora* are chemotactic and can swim to plant roots to establish new infections. The formation of sporangia in soil has been studied with several species of *Phytophthora* and generally has been found to follow one of two patterns (8). Some species require a drained soil, with matric potentials less than −20 millibars (mb, 1000 mb = 1 bar) for optimum formation, while other species appear to require flooded soil (matric potential = 0) (8). If these specific water requirements are not satisfied, sporangium formation is significantly reduced. Additionally, once sporangia have formed, their ability to germinate indirectly by release of zoospores also has exacting water requirements. In experiments with *P. megasperma* and *P. cryptogea* (13), optimum release of zoospores occurred only in fully-saturated soil, and even a slight drainage of the soil, to matric potentials of −5 or −10 mb, caused a significant reduction in the number of zoospores released. Finally, the ability of zoospores to swim through soil and infect plant roots is dependent upon the availability of large ($\geq$300 um) water-filled pores (6). Pores of the required diameter would only be filled with water in soils that are at, or very near, complete saturation (6).

While conditions of high soil moisture have been shown to favor important stages in the life cycle of *Phytophthora* spp., stimulation of the pathogen may only partly explain disease enhancement in flooded soil. Recent work has shown that host factors associated with oxygen deficiency can also play a significant role in disease development. Oxygen quickly becomes deficient in flooded soils when soil pores are filled with water rather than air, although the degree of anaerobiosis which develops is mediated by drainage properties of the soil, distribution and continuity of soil pores, and respiration of roots and microorganisms (17). Conditions of oxygen deficiency can be injurious to roots, and recent evidence shows that such stress can predispose plants to infection by *Phytophthora* spp. In the case of Phytophthora root rot of citrus (21), plants grown in soil infested with *P. parasitica* and *P. citrophthora* and exposed to conditions of low soil oxygen (partial pressure 10-13 mm Hg or $\leq$0.3 mm Hg) had higher percentages of root decay than plants exposed to normal levels of soil oxygen (partial pressure 152 mm Hg). While these experiments showed that oxygen deficiency could increase disease severity, the authors considered it to be only a secondary contributing factor, which prevented regeneration of roots decayed by *Phytophthora* and thus made plants less able to tolerate the effects of chronic root rot (21). They believed that enhanced activity of the pathogen, as a function of irrigation treatment, was the major factor which influenced severity of disease. However, other workers used a slightly different approach to more completely separate host effects from pathogen effects, and showed that stresses encountered by roots in flooded soil could indeed influence their initial susceptibility to infection. In experiments with Phytophthora root rot of alfalfa, seedlings were exposed to flooded soil conditions for periods ranging from 1-5 days prior to inoculation with zoospores of *P. megasperma*, and it was found that the longer plants were held in flooded soil, the more severe the disease which resulted (11). Likewise, exposure of 1-year-old rhododendrons to flooded soils increased their susceptibility to infection by *P. cinnamomi* (3). When plants of the ordinarily resistant cultivar Caroline were subjected to 24 or 48 hr periods of flooding immediately before inoculation, there was a significant increase in the severity of resulting disease symptoms (Fig. 1).

In both the alfalfa (11) and rhododendron (3) examples, roots were exposed to intervals of flooding before the pathogen was introduced, so the primary effect of flooding was clearly to act on roots and somehow increase their susceptibility to disease. While our knowledge of how this occurs is incomplete, there is some evidence indicating possible mechanisms. In work describing predisposition of alfalfa to Phytophthora root rot, Kuan and Erwin (11) examined roots recovered from plants exposed to flooded soil treatments and found that cracks and ruptures developed in epidermal tissues, resulting in the exudation of large amounts of sugars and amino acids. Such substances are known to stimulate the chemotactic response of zoospores (25) and upon ex-

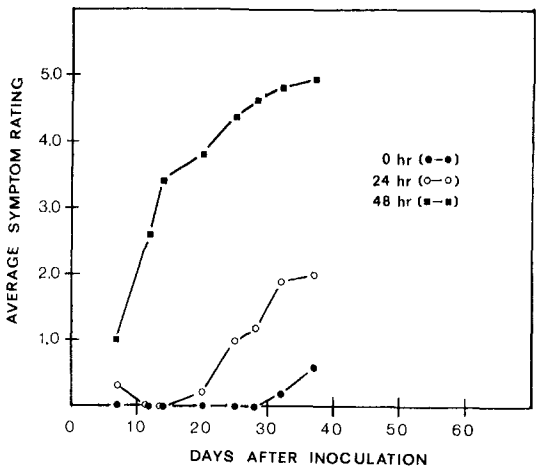

Fig. 1. Effect of preinoculation flooding on the development and severity of Phytophthora root and crown rot of the rhododendron cultivar Caroline. Plants were held under flooded soil conditions for 0, 24, or 48 hr prior to inoculation with zoospores of *Phytophthora cinnamomi*. Disease symptoms were rated on a scale of 0 (healthy plant) to 5 (dead plant), and each point represents the mean for 5 plants (LSD = 2.36 at P = 0.05). (From Baker and MacDonald, 1981).

amination, the investigators found that significantly greater numbers of zoospores were attracted to roots exposed to prolonged flooding (11). Thus, they hypothesized that alfalfa plants subjected to flooded soil conditions were predisposed to Phytophthora root rot as a result of stress-induced injuries which stimulated the attraction of zoospores and maximized the severity of infection. However, this hypothesis may not entirely explain the observed increase in disease. In recent experiments on Phytophthora root rot of safflower, Duniway and Heritage (personal communication) found that when hydroponically-grown plants were inoculated first and then exposed to varying degrees of oxygen stress (by bubbling gasses of known composition through the root systems, lesions developed and enlarged most rapidly on oxygen-stressed roots. This work suggests that oxygen stress may alter the normal defense mechanisms of the host.

Just how widely these findings will apply to other plant species is not known. Recent experiments with cherry seedlings (24) showed that a 48 hour flooding treatment prior to inoculation had no effect on disease development, whereas flooding for the same length of time after inoculation resulted in severe disease. Whether these results indicate a simple enhancement of pathogen activity, or some unidentified interaction between host and pathogen is a question which needs further investigation. Certainly the sensitivity of plant roots to periodic flooding could vary greatly depending upon species and season and this could be a determining factor in predisposition. Clearly, however, the conditions which exist in flooded soils not only favor pathogen activity, but in some cases (3, 11, Duniway and Heritage, unpublished) can predispose roots to severe infection.

Water Stress

Water stress develops in plants as a result of inadequate supplies of soil water and can influence almost every aspect of plant growth including anatomy, morphology, physiology and biochemistry (10). A number of examples, particularly among canker pathogens of woody plants, are available which demonstrate water stress to be a predisposing factor in disease (18). Indeed, the evidence available has suggested (19) that there may be critical levels of plant water stress, at water potential values of −12 to −15 bars (as opposed to water potential values of −4 to −6 bars for well-watered, fully turgid plants), where significant changes in host susceptibility occur. However, while examples of drought stress predisposition have been known for some time (18, 19), only recently have such stresses been shown to be a predisposing factor in Phytophthora root rots. The first example of predisposition involved Phytophthora root rot of safflower (7), where exposure of the susceptible cultivar Nebraska 10 to a cycle of water stress prior to inoculation was found to result in much more severe root rot than when plants were not stressed prior to inoculation. Furthermore, when plants of the genetically-resistant cultivar Biggs were exposed to the same treatments, water stress broke down their resistance and severe root rot developed (7).

Using similar experimental methods, in which irrigation water was withheld from plants to impose a desired level of water stress prior to inoculation,

Blaker and MacDonald (3) demonstrated that water stress could also predispose woody plants to Phytophthora root and crown rot. They found that one-year-old plants of the rhododendron cultivar Purple Splendour, which is highly susceptible to *P. cinnamomi,* were severely diseased following inoculation, regardless of prior irrigation treatment (Fig. 2). In contrast, plants of the cultivar Caroline, which is resistant to disease, showed no visible symptoms for as long as 90 days after inoculation if they were irrigated regularly, but developed obvious and increasingly severe symptoms (Fig. 2) if they were first exposed to water stress sufficient to cause leaf wilt (at leaf water potentials of −16 to −20 bars).

The levels of water stress achieved by withholding irrigation in both the safflower (7) and rhododendron (3) examples were sufficient to cause leaf wilt, but not permanent injury to the plants. Indeed, the stresses were considered representative of what plants sometimes encounter during cultivation. While the pathogens were not present in the soil during the stress cycles, available evidence indicates that similar levels of water stress would have no adverse affect on several species of *Phytophthora*. For example, sporangia of *P. cryptogea* can tolerate drying in soil to much lower water potential values than those which predisposed safflower to disease (7) and still be capable of releasing motile zoospores upon subsequent wetting (14). Furthermore, upon irrigation of plants to relieve water stress, soil conditions temporarily become optimum for zoospore release and movement in soil (6, 13), in the presence of stress-injured roots.

In the two examples of predisposition known (3, 7), there is not enough direct evidence of events to form a hypothesis describing how water stress resulted in predisposition. Water stress is known to injure cell membranes and increase their permeability (9), and it is possible that abnormally large amounts of chemotactically-active substances may leak from roots immediately following irrigation, and stimulate zoospore attraction. However, limited evidence with safflower (7), suggests that drought stress may also cause changes in roots that alter their defensive response to pathogenic invasion. Whether similar levels of stress could predispose tree species to Phytophthora root rots is not known, but there is good evidence showing that trees can be predisposed to various branch canker pathogens as a result of water stress (18), and that predisposition probably results from stress-induced changes in plant metabolism. Thus, water stress may be an important factor in the occurrence or severity of Phytophthora root rots on some trees.

Salinity Stress

A third form of stress which has been associated with Phytophthora root rots is excess salinity, which is a serious problem in many irrigated areas of the southwestern United States. Many factors contribute to the build-up of salts in soil, with poor quality of available irrigation water, application of fertilizers or soil amendments, and inadequate leaching of affecting soils being among the more important. While many morphological and physiological disturbances in salt-stressed roots have been described over the years (2), information concerning the impact of

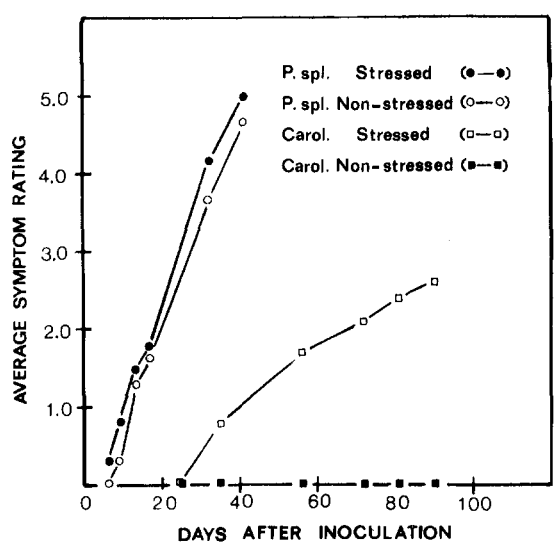

Fig. 2. Effect of a preinoculation drought stress on the development of Phytophthora root and crown rot in rhododendron cultivars Purple Splendour (P. spl.) and Caroline (Carol.). Stressed plants had leaf water potentials ranging from −2 to −6 bars. Disease symptoms were rated on a scale of 0 (healthy plant) to 5 (dead plant), and each point represents the mean for 5 plants (LSD = 1.57 and P = 0.05). (From Blaker and MacDonald, 1981).

these stresses on disease interactions has been slow to develop. Apparently the first systematic study of this question was reported in 1949 (1), and involved the role of excess fertilizer salts on seedling diseases of tomato. Seedlings grown in soil infested with *Rhizoctonia solani* or *Fusarium oxysporum* f. sp. *lycopersici,* were found to have significantly more disease when stressed by high concentrations of fertilizer salts, and the increase in disease was attributed to a relative growth advantage held by the pathogens over the host under conditions of osmotic stress.

In more recent experiments (12), salinity stress has been shown to directly affect plant roots and increase their susceptibility to disease. Rooted chrysanthemum cuttings were grown hydroponically in crocks containing a nutrient solution and given 24 hour pulse-exposures to salinity stress by adding NaCl directly to the nutrient solutions. After a 24-hour exposure to 0.1M or 0.2M NaCl, plants were transferred back to fresh nutrient solution and both stressed and nonstressed plants were inoculated by adding zoospores of *P. cryptogea* into the crocks. Severe symptoms of disease rapidly developed on plants exposed to the highest level of salinity, while plants which had not been stressed prior to inoculation had relatively few disease symptoms (Fig. 3). Plants exposed to intermediate levels of stress developed intermediate levels of disease.

Although the levels of stress employed in these experiments were fairly severe, they were considered a reasonable approximation of stresses which plants might encounter in saline soils between cycles of irrigation (12). Furthermore, although evidence is limited, *Phytophthora* spp. apparently can carry out most phases of their life cycle, including mycelial growth, sporangium formation, and zoospore release, under very similar conditions of salinity (20, Blaker and MacDonald, unpublished). Because the experiments involved the application of stress to roots prior to inoculation, salinity stress clearly predisposed them to severe disease, and the effects of salinity stress on roots appeared very similar to those of oxygen or drought stress. For example, high levels of salinity are known to disrupt the selective permeability of cell membranes (4) and could influence chemotaxis of zoospores. Indeed, large numbers of zoospores were observed to attach to stressed roots, which suggested either an enhanced attraction or more efficient binding of zoospores (12). However, similar to the work with oxygen and drought stress, there also is evidence suggesting salinity stress may cause some change in root tissues which inhibit their ability to restrict or slow pathogenic invasion (Swiecki and MacDonald, unpublished).

Just how widely predisposition to Phytophthora root rots might occur in salt-affected regions is presently unknown. Salinity stress is considered an important factor influencing growth and development of a wide range of agricultural and ornamental plants in some areas, and many trees and other woody species are among plants known to be sensitive. Furthermore, Phytophthora root rots are known to be problems on trees, for example citrus, in areas where salinity stress is a significant problem. Thus, while careful documentation is unavailable, the probability of salinity-stress predisposition in nature appears great.

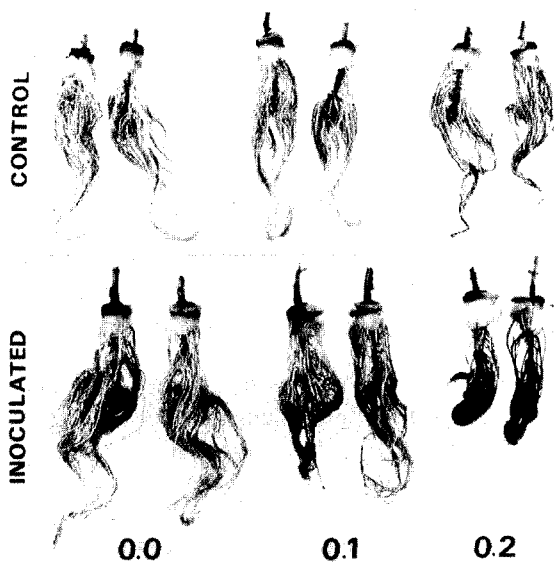

Fig. 3. Chrysanthemum roots grown in half-strength Hoagland's solution and given a 24-hr pulse exposure to (from left to right) 0.0, 0.1, or 0.2 M NaCl-amended solution. Root systems across the top are non-inoculated controls, while those across the bottom were inoculated with 10^6 motile zoospores of *Phytophthora cryptogea* immediately upon relief of the stress. (From MacDonald, 1982).

Summary

The experimental evidence reviewed here shows unequivocably that stresses to plant roots caused by oxygen deficiency, water stress, or salinity, can predispose roots to infection and disease caused by *Phytophthora* spp. These findings are significant because they show that environmental factors which either had not previously been recognized, or were believed only to influence pathogen activity, actually exert a determining role in tissue susceptibility. Furthermore, the levels of stress which have been identified as critical for predisposition are believed to be representative of stresses which plants sometimes encounter during normal cultivation and, in the absence of *Phytophthora* spp., would not cause significant damage to plants. While these stresses can greatly increase the susceptibility of plants to severe root rot, they do not appear to adversely affect *Phytophthora* spp. Indeed, in the case of flooded soils, some stages in the life cycle of *Phytophthora* spp. are actually stimulated. While the mechanism of predisposition has not been characterized at the metabolic level for any of these stresses, there apparently are some general features in common. Following the exposure of roots to stress, the number of zoospore cysts which bind to them significantly increases. This "inoculum capture" could greatly increase the number of initial infection sites. But, in addition to this, intervals of stress also appear to interfere with a plant's ability to reduce or block pathogen spread within the tissue. Hence, following a period of stress, either or both of these factors may be involved in determining disease severity.

Just how widely this work, which to a large extent has involved herbaceous plants, will apply to Phytophthora root rots of trees and other woody plants is not known. However, good evidence has been presented which links a variety of stresses such as drought, temperature, and even defoliation (18) with predisposition of trees to various canker pathogens. Thus, the defense mechanisms in aerial portions of woody plants are known to be impaired by stress, and it seems likely that roots would be similarly affected. Work is in progress in several laboratories to examine these questions and to define the limits of stress which can be tolerated by plants without affecting their susceptibility to disease. Fortunately, among the stresses which have been identified as important in predisposition, each can be controlled to some extent through environmental manipulations. This makes a complete knowledge of their role in disease very important.

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CORRECTIONS

The following paragraph was omitted from the paper by Winand K. Hock on Sevin: a Controversial Insecticide. J. Arboric. 8(2): 47-49. It should be included on page 49, left-hand column, five paragraphs down, just prior to the one beginning "New Jersey Superior Court Judge." Please mark **insert paragraph page 223** at this point.

The report concluded that there was **no** link between spraying with Sevin and birth defects. The rate of birth defects in Cape May County towns was actually higher in 1977 when Sevin was not used than in 1979 when it was used in a gypsy moth control program. In four towns in Cape May County where Sevin was sprayed in 1979, the rate was 19.76 birth defects per 10,000 live births while the rate of birth defects in 13 unsprayed towns was slightly higher at 22.27. Monmouth County shows a similar drop in the rate of birth defects from 1977 to 1979. Only in Morris County did the rate of birth defects show a slight increase between 1977 when no spraying was done and 1978 and 1979 when Sevin was used.

Two changes should be made in the paper by Fraedrich & Ham on Wood Chip Mulching, J. Arboric. 8(4): 84-89.

(1) On page 86, Figure 1, the height growth should be in meters (not cm) from bottom to top **0.2, 0.4, 0.6, 0.8, and 1.0** *(not 0.5, 1.0, 1.5, 2.0, 2.5).*

(2) On page 87, second paragraph, the fourteenth line should read **0.057g/170 cm^3** *(not 0.57g/170 cm^3).*