

Effects of Flooding on Plant Disease

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I.	Introduction	222
	A. Oxygen in Soil Pores	222
	B. Water in Soil Pores	224
II.	Flood-Prone Soils	227
	A. Profile Characteristics	227
	B. Physicochemical Characteristics	228
III.	Flooding Effects on the Host Plant: Morphology and Function	228
	A. Roots	229
	B. Shoots	230
IV.	Predisposition Effect of Waterlogging	230
	A. Root Surface	230
	B. Release of Exudates	236
V.	Flooding Effect on Plant Pathogens	238
	A. Fungi	238
	B. Nematodes	241
VI.	Dissemination of Pathogens by Flooding	246
	A. Lateral Dispersal on the Soil Surface	246
	B. Vertical Movement in the Soil	247
VII.	Root-Pathogen Interactions	248
	A. Root Attraction	248
	B. Root Infection by Zoospores	252
VIII.	Plant Water Stress as a Predisposing Factor	254
IX.	Control of Disease by Flooding	255
	References	256

I. INTRODUCTION

A. Oxygen in Soil Pores

In discussing flooding in relation to plant disease, one is faced immediately with problems in terminology. The concept of flooding encompasses a range of soil conditions, and the notion of disease incorporates a variety of plant dysfunctions. The severity and duration of flooding influence disease incidence, and each disease manifests itself at a particular threshold of flooding severity. Finally, the diverse nature of soils renders difficult the universal application of unique definitions, empiricisms, and theories. Certain principles can, nonetheless, be established. The following discussion of flooding and disease interaction is presented from a soils-oriented perspective.

The most negative effect of soil flooding derives from the impact of high water content on soil oxygen (Durbin, 1978). The status of soil O_2 may be characterized as a capacity factor, an intensity factor, or a rate factor. Although each is frequently treated singly, to characterize soil O_2 status all three must be defined for the best characterization of the soil- O_2 system.

As a capacity factor soil O_2 , which is a component of soil air, is inferred from simple descriptions of the three-phase soil physical model. In describing soil O_2 status with capacity factors alone, it is assumed that O_2 concentrations and O_2 diffusion rates in soil are not limiting. Some of the capacity factors most frequently calculated are

$$\text{Porosity (or free space) } f: \quad f = (V_a + V_w)/(V_s + V_a + V_w) \quad (1)$$

$$\text{Void ratio } e: \quad e = (V_a + V_w)/V_s \quad (2)$$

$$\text{Saturation ratio } \theta_s: \quad \theta_s = V_w/(V_a + V_w) \quad (3)$$

$$\text{Air-filled porosity } f_a: \quad f_a = V_a/(V_s + V_a + V_w) \quad (4)$$

$$\text{Volume wetness } \theta: \quad \theta = V_w/(V_s + V_a + V_w) \quad (5)$$

where V_a , V_w , and V_s are the volumes of soil air, soil water, and soil solids, respectively.

An excellent discussion of these fundamental parameters and their relationship to one another was presented by Hillel (1980). Various investigations have related plant performance to capacity factors (Bushnell, 1953; Miller and Mazurak, 1958; Flocker *et al.*, 1959; Willhite *et al.*, 1965). Each of these parameters in some way describes the capacity of the soil to hold air, but reveals nothing about the nature of the air or its transport properties.

The major constituents of soil air and the ambient atmosphere are N_2 , O_2 , and CO_2 . About 78% (by volume) of both is nearly constantly composed of N_2 .

However, whereas atmospheric O_2 is nearly constant at 21%, soil air varies between nearly 21 and nearly 0% (Russell and Appleyard, 1915; Boynton and Reuther, 1938). When O_2 in soil falls below 21%, the drop usually corresponds closely to the increase in CO_2 . Mean annual CO_2 concentration in the atmosphere is currently slightly above 0.03% (Revelle, 1982). In soil, however, CO_2 concentrations can exceed 12%. Furthermore, O_2 concentration generally declines and CO_2 concentration generally increases with depth in the soil profile.

Other gases (primarily by-products of anaerobic metabolism such as methane or ethylene) can also occur, from trace amounts to a few percent in soils as the redox potential of the soil environment becomes more negative. Although CO_2 and these trace gases usually occur in relatively small proportions to the other gases present, they frequently induce pronounced plant physiological responses, even at low concentrations.

Because soil air is composed of numerous constituents, the need to determine intensity factors (concentrations or partial pressures) of the particular gases present is important for three reasons: (1) If the concentration of O_2 is low (relative to ambient air), this indicates there are dynamic processes active in the soil profile consuming soil O_2 ; (2) determination of significant concentration of gases known to affect plant response can foreshadow or explain changes in growth, physiology, and production of plants; and (3) O_2 concentration indicates the level of chemical activity of soil O_2 , in essence providing an indirect assay of the oxidation-reduction status of the soil environment.

Although intensity factors describe the relative amounts of gases present in the soil, they do not indicate if the rate of O_2 consumption in the rhizosphere can be satisfied by the rate of O_2 movement through the air-filled soil pores. Understanding the balance of these two rate factors provides the basis of modern conceptual models of soil aeration. It is from these models that understanding of flooding phenomena is derived.

Although O_2 movement into the soil profile can be attributed to changes in soil temperature, surface turbulence, variation in barometric pressure, and physical displacement by and dissolution from infiltrating water, the most active mechanisms by far is diffusion from the ambient atmosphere (Russell, 1952). Similarly, gases produced in the soil are exhausted primarily by diffusion to the ambient atmosphere along concentration gradients.

Diffusion of O_2 through soil to sites of respiration by plant roots and microorganisms is governed by such factors as concentration differences along the diffusion pathway, length and tortuosity of the pathway, and diffusion coefficients of the media encountered in diffusing from source to sink. The last factor is particularly important, because O_2 diffuses 10^4 times more slowly through water than through air (Greenwood, 1961), and only one-fourth as rapidly through dense protoplasm as through water (Krogh, 1919; Warburg and Kubo-

witz, 1929). The physical principles governing these processes are described in Fick's law:

$$J = D_{\epsilon} \frac{dC_{\epsilon}}{dx} \quad (6)$$

where J is gas flux per unit cross section of soil, C_{ϵ} the concentration of the particular gas in the gas phase of the medium, and D_{ϵ} the apparent diffusion coefficient of the gas in the medium (Stolzy *et al.*, 1981).

Refinements and complex adaptations of Fick's law have been used to describe both gas movement and O_2 use by soil organisms. Expansion of this conceptual base has been reviewed by Armstrong (1978, 1979), Bouldin (1968), Cannell (1977), Currie (1970), Grable (1971), Greenwood (1971, 1975), Meek and Stolzy (1978), Stolzy (1974), Stolzy *et al.* (1981), Luxmoore and Stolzy (1972a), Vartapetian (1973), and Vartapetian *et al.*, (1978).

Aeration and flooding phenomena cannot, however, be easily dealt with in the confines of a single conceptual base. The same factors that complicate analysis of all biological phenomena confound our understanding of flooding and, more specifically, the interaction of flooding and disease. They include spatial, temporal, thermal, chemical, and biological variability. Finally, although aeration plays the single most dramatic role, numerous other phenomena associated with abundant soil water influence the flooding-disease interaction. These phenomena range from simple hydration effects to changes in active and passive motility of soil-borne pathogens.

B. Water in Soil Pores

Because of the dipolar nature of the water molecule and the predominantly negative charge of soil minerals, particularly clay minerals, water is readily adsorbed on soil particle surfaces. Furthermore, the smaller the interparticle distance, the greater the proportion of the water molecules in soil pores affected by surface attraction. As water is pulled across particle surfaces by surface attraction during adsorption, a drop in pressure is created behind the advancing meniscus, in much the same way that pressure drops behind a piston drawn out of a closed cylinder. Water behind the meniscus advances under the pressure gradient until the attractive forces at the wetting front are in equilibrium with the hydrostatic pressure and cohesive forces of the advancing water. This phenomenon, capillarity, is the foundation on which much of the physics of soil flooding is based.

The principles of capillarity explain the difference in water retention among soils of like texture with differing pore geometry and among soils with different pore geometries caused by textural differences. Soil water potential ψ (the chem-

ical potential of soil water) expresses the energy status (capacity or "potential" to do work) of water in soil relative to pure free water in the same position. Soil water usually has a negative potential because it is held in soil by forces of adsorption, cohesion, and solution and therefore has less capacity to do work than free water at the same position. The less water there is in soil, the more tightly the remaining water is held, and therefore the lower (more negative) its ψ . The most easily determined component (and usually the largest in most agricultural soils without salinity problems) is the soil matric potential ψ_m . It is that part of the total ψ explainable by the surface attractions of soil particles and plant roots as arranged in the soil profile (Taylor and Ashcroft, 1972). As mean pore size decreases, θ_s increases for a given ψ_m , accounting for the difference in water-retention curves for soils of differing textures and levels of particle aggregation. This principle also dictates that on desorption, the smallest pores empty last.

Consequently, it is erroneous to consider soils as homogeneous bodies of uniformly distributed pore water. Particle surfaces in close proximity to macropores seldom lose contact with the gaseous phase even at ψ_m somewhat above field capacity (FC). Certain pores within the soil mass, however, are rarely exposed directly to soil air. Particle surfaces near the smaller micropores or near the center of aggregates may remain undrained even at potentials approaching 1 bar. Therefore, flooding of discrete pores occurs over a continuum of conditions. Some pores are nearly always water filled in almost all soils. This results in the simultaneous existence of regions of aerobic and anaerobic conditions throughout the soil profile, dependent on sink strength and limitations to diffusion (Currie, 1962; Letey and Stolzy, 1967). This situation also explains detection of small amounts of anaerobically derived chemicals even in soils that are otherwise well drained (Lynch, 1975; Primrose, 1976; Hunt *et al.*, 1980, 1982; Smith, 1980).

On inundation of the soil profile from surface flooding, the hierarchy (with respect to pore size) of water entry into the profile is the reverse of desorption. Because of the vastly greater saturated hydraulic conductivity of macropores, water rushes first into and through the large continuous pore spaces. As this occurs, large volumes of soil air are displaced from the macropores, while numerous small pores are left with trapped air that slows subsequent entry of water. Water continues to move into the profile until the limits of retention at FC are reached for the depth of water applied, or until a restricting plane is encountered, slowing the advance of water and resulting in saturation of the soil above the less permeable layer.

For a horizon of large pores overlying a horizon of smaller pores, if the rate of water application at the soil surface is lower than the saturated hydraulic conductivity of the overlying horizon (but greater than that of the lower horizon), water flows downward in the unsaturated state until the interface is encountered. On

penetrating the lower horizon, its flow is reduced to a rate equal to its saturated hydraulic conductivity. Because water is arriving at the interface faster than it can flow through the lower horizon, it begins to accumulate, saturating the soil above the interface. If application of water continues, the zone of saturation progresses upward, eventually ponding at the surface.

To understand why flooding of pores occurs when a horizon of relatively small pores overlies one of larger pores, one must turn again to capillary phenomena. This is all the more remarkable inasmuch as it can occur to a limited extent even if the rate of water application at the soil surface is less than the saturated hydraulic conductivity of either horizon. As explained previously, surface forces and capillarity lower soil water pressure to a value below atmospheric pressure. When a soil pore abruptly increases in diameter, the situation is analogous to the pore's draining into an open void. Because water in the pore is at a pressure lower than the air pressure in the void, the meniscus is curved inward, away from the side of higher pressure. Flow into the void cannot proceed until the pressure in the smaller pore exceeds atmospheric pressure. Sufficient pressure is finally achieved when, again, water ponds above the interface of the two horizons as a result of the temporary cessation of flow. This backing up of water results in a zone of flooded pores above the coarser-textured horizon. Eventually, sufficient pressure is achieved to counter the negative ψ_m . The water pressure in the small pores at the interface finally exceeds atmospheric pressure, and water flows into the larger pore.

Ironically, gravel is often placed at the bottom of pots or planting beds, ostensibly for drainage. This can result both in flooding on irrigation with less water for a given volume of soil, and in less water storage in the reduced soil volume for plant use between waterings.

On introducing consideration of living organisms in flooded profiles, the situation is further complicated regardless of the indicator selected to define aeration. Average profile O_2 status may be irrelevant to the particular O_2 status at a microsite near a root hair or single-celled microorganism. Virtually all current technology integrates O_2 status over soil volumes more representative of macropores than micropores. Biological sinks for O_2 , and therefore soil O_2 status, may vary by one or two orders of magnitude over a few micrometers distance from respiring cells. The mean status of aeration in the soil mass is therefore less important than the likelihood of encountering sites where the rate of O_2 supply is insufficient to meet the potential respiratory demand of soil organisms. Differences in the sampling volumes of various aeration sensors and actual differences in soil O_2 status over short distances within the soil led Flüher *et al.* (1976) to conclude that soil aeration is most appropriately characterized by a statistical expression of microsite spatial heterogeneity. Application of this concept was developed in greater depth by Stolzy *et al.* (1981).

FLOOD-PRONE SOILS

A. Profile Characteristics

The frequency and duration of flooding have a marked impact on soil properties and plant response. Flooding problems on a field scale occur most commonly on relatively level land with restricted surface or internal drainage (due either to fine soil textures with low saturated hydraulic conductivity or to shallow water tables). Soils with these properties are characteristically found in low-lying river deltas or floodplains, on remnant or recessional lacustrine formations, and along low-lying maritime coastal plains. Parent materials in these soils (particularly the first two groups) are frequently dominated by expanding lattice 2:1 clay minerals. The pore geometry of these shrink-swell soils varies immensely with ψ_m . Often, the higher the clay content, the smaller the mean pore size at saturation and the greater the likelihood of extensive and deep cracking when ψ_m is only slightly lower than ψ_m at FC. The complexity and variability of the pore geometry in these soils make it difficult to determine the degree or extent of O_2 depletion in the soil profiles in the field at an acceptable level of statistical reliability.

In the newly adopted comprehensive soil taxonomy (Soil Survey Staff, 1975), there is no soil order in which flooding cannot occur, although the properties of certain soil orders are such that flooding can be expected to occur naturally more often. This distinction is apparent in the absence of an Aquic subgroup in the order Aridisols, for example. However, Histisols are also without an Aquic subgroup; in this case, flooding and its impediment of organic matter oxidation is a formative factor that occurs throughout the entire order. Soil flooding and its role in soil genesis and classification are discussed in greater detail by Ponnampetuma (Chapter 2 in this volume). As a diagnostic tool, several profile characteristics are ready indicators of frequent flooding in nature.

Where soil flooding is frequent and prolonged, the lower profile usually remains reduced. Iron and manganese are present in ferrous and manganous forms and impart a deep gray color, frequently grading into a bluish cast. This condition is referred to as gleying (Soil Survey Staff, 1951). Frequently, flooded soils are also relatively high in organic matter in their surface horizons, rendering them dark or black in color. Where high soil temperatures result in oxidation of surface organic matter between periods of inundation, the flooding proneness of the soil may still be evident in the stratified deposition of parent materials in lenses of various thickness. Horizons that are intermittently flooded for prolonged periods and that have irregular internal drainage are frequently mottled. In diagnosing site susceptibility to flooding or flood-induced diseases, all of these profile characteristics should be examined.

B. Physicochemical Characteristics

Where soils are persistently flooded, the physiochemical characteristics of the soils that have developed *in situ* are basically those associated with steady-state reducing environments. Free water is likely to be present at a shallow depth in the soil profile, and the remaining profile may be within the capillary fringe, close to saturation. Free O_2 is nearly absent even near the soil surface and is certainly extinct at some modest depth within the profile. Metallic cations such as iron and manganese exist in their lower valence states, and oxidation-reduction potential E_h , a measure of electron availability in soil, is low. In highly aerated (oxidized) soils, E_h is of the order of +0.6 V. In extremely anaerobic (reduced) soils, E_h can be as low as -0.2 V. The E_h is especially dependent on soil pH as well as on iron and manganese content. The concept of E_h has been developed in detail by Novozamsky *et al.* (1976) and by Bohn *et al.* (1979). Application of the concept of E_h has also been explained by Russell (1976) and is discussed in detail by Ponnampertuma, (Chapter 2 in this volume).

When a soil is flooded, characteristic shifts occur in populations of soil organisms. Algal populations may be large near the surface, and there is frequently a larger than normal microfauna component. Higher-order plants almost certainly are composed largely of flood-tolerant species.

Where soils are intermittently flooded for periods of days or weeks, the profile may never achieve a steady state. Depending on the initial organic and inorganic properties and the initial O_2 availability within the soil at the beginning of each flooding episode, the soil profile will pass through a range of transient intermediate stages. The duration and nature of each intermediate stage will depend largely on soil temperature, amount of fresh organic matter present, initial soil microflora component, and nature of the higher plants growing in the soil. Rice, for example, introduces significant amounts of O_2 into the soil profile in paddy culture by diffusion of atmospheric O_2 from shoots to the highly porous root systems and by release of some of the O_2 to surrounding soil. The balance of these inorganic, organic, and biological inputs can explain the falling E_h of the system for varying lengths of time at discrete redox potentials as the profile depletes each pool of successively less willing electron acceptors (Patrick and Mikkelsen, 1971; Russell, 1976). These physiochemical and biochemical considerations are presented in detail by Ponnampertuma (Chapter 2 in this volume).

III. FLOODING EFFECTS ON THE HOST PLANT: MORPHOLOGY AND FUNCTION

Several reviews have detailed the morphological and physiological changes that occur in higher plants as a result of flooding (Williamson and Kriz, 1970; Stolzy, 1972; Drew and Lynch, 1980; Bradford and Yang, 1981; Kawase, 1981;

Wiedenroth, 1981; Campbell, 1981; Armstrong, 1981). These changes are in great part responsible for a given species' individual level of susceptibility or resistance to flood injury and related disease. Several specific predisposing factors are discussed later in this chapter, and most of the general consequences of flooding on plant morphology and physiology are discussed in other chapters in this volume by Jackson and Drew (Chapter 3), Kozłowski (Chapter 4), Kozłowski and Pallardy (Chapter 5), and Reid and Bradford (Chapter 6). A few specific effects are briefly emphasized here.

A. Roots

When a root channel is flooded, roots experience an immediate reduction in O₂ supply. One of several consequences may result. In the least severe scenario, root respiration, deprived of free O₂, proceeds along a fermentative pathway, rapidly consuming the available pool of stored carbohydrates—the Pasteur effect (Wiedenroth, 1981; Bertani *et al.*, 1981; Wiebe *et al.*, 1981). Instead of CO₂, alcohol is the predominant by-product released, and the relative amount of energy released has been estimated to be as low as 5% of that liberated for a given amount of substrate via the aerobic pathway (Wiedenroth, 1981). Wiebe *et al.* (1981) discussed numerous alternative pathways, including the reduction of inorganic compounds such as sulfur and production of other by-products, such as methane.

Active uptake of nutrients is greatly diminished as a result of slowing of energy conversion. In the early stages of anaerobiosis (Drew and Sisworo, 1979; Trought and Drew, 1980a,b), mineral requirements of immature aerial plant tissue are met by mobilization from more mature tissue. The substrate requirement of roots is now so elevated that it cannot be met by translocation from shoots alone. Consequently, less resistant cellular constituents are metabolized in place. The latter eventually results in development of lysigenous zones of intercellular voids. These voids formed in the roots allow the diffusion of O₂ from the shoots to active root tissue. This ultimately is the mechanism through which a certain level of normal plant functioning is able to resume (Jensen *et al.*, 1969; Luxmoore and Stolzy, 1966, 1972a,b; Yu *et al.*, 1969; Varade *et al.*, 1970, 1971; Luxmoore *et al.*, 1971, 1972; Papenhuijzen and Roos, 1979; Benjamin and Greenway, 1979; Konings and Verschuren, 1980; Stelzer and Laüchli, 1980; Drew *et al.*, 1980; Kawase and Whitmoyer, 1980; Konings, 1982). Oxygen diffuses more freely through the newly created root air spaces from shoots or better-aerated portions of the root system, internally aerating the submerged portions of the root system.

When flooding is complete and root systems are less adaptable, or respiratory demand is too large to be met by a shift in respiratory pathway, root systems become necrotic. The necrotic tissues lose physical integrity. Such root necrosis

is often termed root pruning. In addition to providing a vector for pathogen entry, root pruning also impairs physiological recovery on drainage of water from the soil profile, by limiting the root volume. The resultant decrease in root-to-shoot ratio impairs soil-nutrient and soil-water extraction in the recovering plant, slowing its subsequent growth and, in most cases, decreasing crop yield.

B. Shoots

Until O_2 is depleted from the flooded soil profile, shoots continue to respond as though irrigated. When soil O_2 is depleted, the chain of events just described ensues. Eventually, shoot physiological activity becomes limited as explained by insufficient water- and nutrient-supplying capability. Other significant responses occur that result from less well understood consequences of flooding. Changes in root membrane permeability and alterations in hormonal composition of the plant produce wilting, leaf epinasty, and stomatal closure (Bradford and Dilley, 1978; Hunt *et al.*, 1981) and stimulate adventitious root development, emanating from stem nodal positions above the zone of saturation (Bose *et al.*, 1977; Wample and Reid, 1978; Drew *et al.*, 1979, 1980; Kozlowski, 1982).

Stomatal closure is not always a simple mechanical response to increased root resistance resulting in lowered xylem pressure potentials (Sojka and Stolzy, 1980). Aside from the physiological implications (decreased CO_2 fixation and decline in photosynthesis), stomatal closure is a negative and almost synergistic reaction to flooding. Once stomata are closed, transpiration declines, which has the net effect of prolonging the flooding episode. Furthermore, stomatal closure restricts gas exchange between leaves and the atmosphere, thus restricting the aerial pathway for internal diffusion of O_2 from the shoots to flooded root systems. Stomatal closure by flooding has been recognized as a means of limiting shoot damage during episodes of air pollution (Stolzy *et al.*, 1961, 1964).

Other, more direct effects of soil flooding on shoot growth also occur. The mechanical support of the root system is substantially reduced in saturated soil. This significantly predisposes the plant canopy to lodging. Lodging brings plant tissue from adjacent plants in contact with one another and, when severe, in contact with wet soil and/or floodwaters. Both effects increase the likelihood of inoculation and spread of disease in the plant canopy. Even in the absence of lodging, if the ground is wet for prolonged periods, the resulting elevation of relative humidity in the canopy favors shoot diseases such as rusts and mildews, which invade the leaf surface when moist.

IV PREDISPOSITION EFFECT OF WATERLOGGING

A. Root Surface

The term *predisposition* has been used since the late 1800's in reference to plant stress in relation to disease (Schoeneweiss, 1975, 1978). The term refers to

host disposition or "proneness" to disease prior to infection. Levitt (1980) divided excess water or flooding stress into primary and secondary stress and indicated that excess water and flooding, although not injurious directly, can cause a secondary O₂-deficient strain. In this section we discuss some studies that demonstrate predisposing effects of flooding on plant diseases and some hypotheses of predisposition mechanisms.

As emphasized by Cook and Papendick (1972), soil water may act on (1) the pathogen, (2) the host plant, and (3) soil microorganisms. The rhizosphere, a narrow zone of soil around the root, is of most interest because of leakage or exudation from plants of various compounds into this zone that promote or inhibit plant pathogens (Curl, 1982). In the rhizosphere, the root is surrounded by a waterfilm that varies in thickness, controlling the O₂ supply for root respiration (Letey and Stolzy, 1967). A second term, rhizoplane, refers to the root surface providing a very favorable nutrient base for a large number of microorganisms.

One hypothesis of the mechanism of flooding stress on root disease suggests that soil saturation changes root tissues, enhancing zoospore attraction and infection. Experiments with safflower (*Carthamus tinctorius* L.) suggested that disease enhancement by flooding was not due entirely to inoculum behavior, but that disease was enhanced by host predisposition (Duniway, 1977b). Occurrence of drought prior to irrigation may also increase the severity of *Phytophthora* root rot in safflower (Duniway, 1979). Therefore, drought could enhance disease development following irrigation, because water stress predisposes the host and water deficiency in the soil increases subsequent production of effective inoculum by the pathogen (Duniway, 1977b).

Phytophthora root rot of alfalfa (*Medicago sativa* L.) is closely associated with excessive rainfall and poorly drained or heavily irrigated soils. Kuan and Erwin (1980) cited "enhanced attraction" as the mechanism by which alfalfa roots were predisposed to infection when subjected to saturation. Using scanning electron microscopy, they showed that after 1 day, breaks in the root epidermal cells occurred on the surfaces of roots grown in saturated soil, whereas the surfaces of roots grown in unsaturated soil were smooth and intact (Fig. 1). Papenhuijzen and Roos (1979) recognized that a recurring question in studies of root development in poorly aerated nutrient solutions is whether the low O₂ concentration is a primary inhibiting factor. In such studies, root growth is inhibited more than expected on the basis of the O₂ measured in the medium. However, O₂ concentration at the root surface is much lower than in the bulk medium because of consumption of O₂ by the root and low diffusion of O₂ inward through the water film around the root. Papenhuijzen and Roos (1979) found several effects after stopping aeration of the nutrient solution. In bean (*Phaseolus vulgaris* L. cv. Berna), starch grains disappeared from the amyloplasts of root-tip cells, small dense lipid bodies formed, and the rough endoplasmic reticulum of cortical cells showed concentric arrangements that

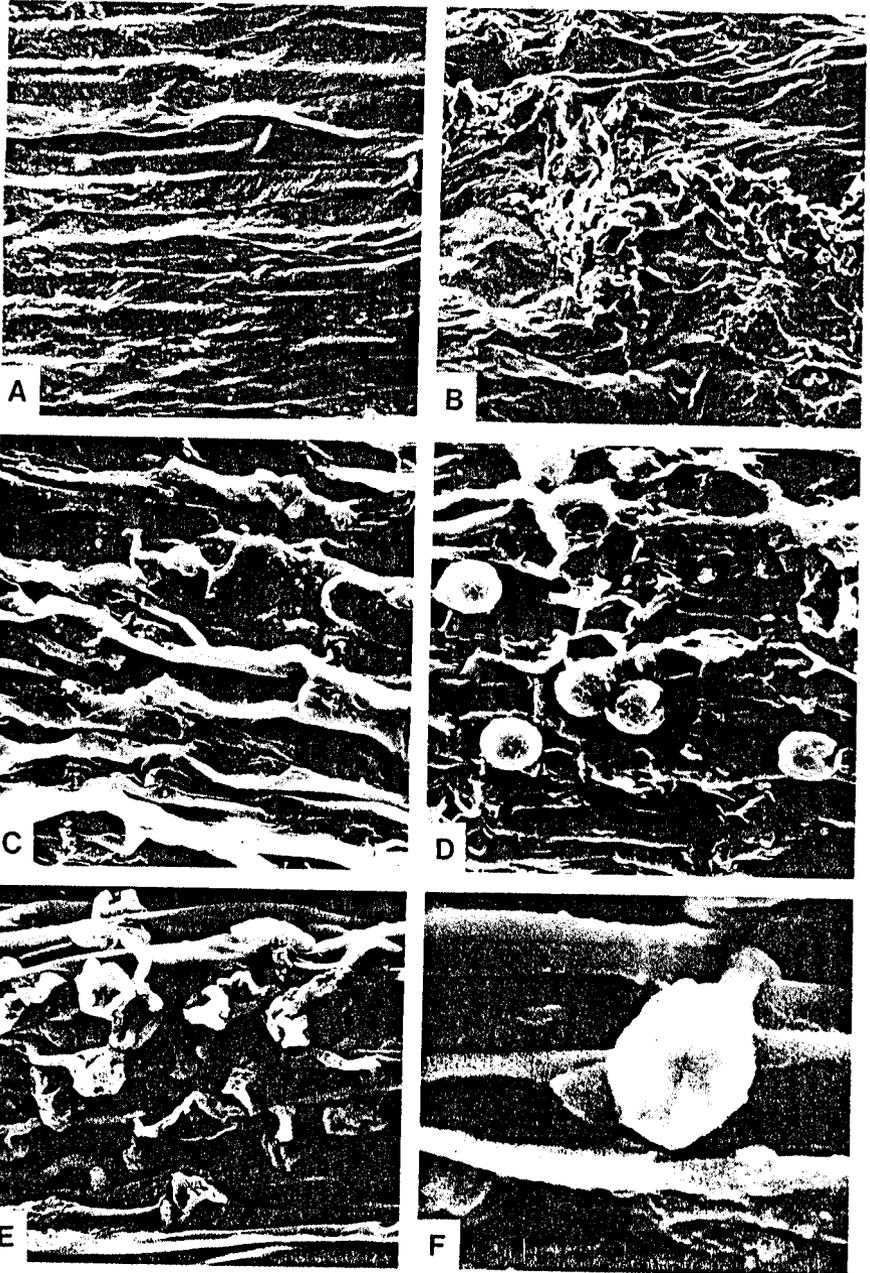


Fig. 1. Scanning electron micrographs of the surface of alfalfa roots (A) Alfalfa roots grown in unsaturated soil (1000 \times). (B) Alfalfa roots grown in saturated soil for 1 day (1000 \times). (C) For 5 days (1000 \times). (D) Zoospores of *Phytophthora megasperma* f. sp. *medicaginis* penetrating a root from saturated soil (1000 \times). (E) Germinated zoospores on a root from saturated soil (1000 \times). (F) Growth of the germinated zoospores into the break in the root surface (3000 \times). From Kuan and Erwin (1980).

were attributed to anoxia. One day after aeration was stopped, cells of the extreme tip of the root axis were dead. After 2 or 3 days, older cells 2–3 mm from the root tip were dead.

Knous and Maxfield (1976) hypothesized predisposition associated with root rot of alfalfa under O_2 stress. They reported that in a field irrigated every 4 days, increase of squalene concentration of roots in the susceptible cultivar Saranac was associated with root-tissue dissolution characteristic of *Phytophthora* root rot. The squalene increase may have resulted from root-tissue predisposition resulting from O_2 stress and not from flooding directly. In comparison, plants in plots irrigated every 10 days had no root rot and showed no increase in squalene.

Effects of waterlogging on concentrations of gases and solutes dissolved in soil water were investigated by Trought and Drew (1980a,b) to determine whether the early disruption in growth of wheat (*Triticum*) was most closely associated with depletion of dissolved O_2 , accumulation of toxins, or changes in nutrient concentrations in the soil water. Injury to shoots and roots was attributed to a decrease in soil O_2 concentration rather than to concentration of inorganic nutrients or accumulation of toxins in the soil water.

Several studies have shown that the apical root meristem stops growing almost immediately in an anoxic soil environment. Using time-lapse photography, Klepper and Huck (1969) and Huck (1970) showed that in less than 3 hr, cells in the region of root elongation died without sufficient O_2 . When the soil was re-aerated, lateral roots branched from the undamaged part of the taproot.

Letey and Stolzy (1967) analyzed the soil and water geometry around the root in relation to O_2 supply at the root surface. Soil O_2 diffusion rate (ODR) from gas-filled soil pore spaces decreased as water-film thickness around the root increased. An earlier study showed that root growth was correlated with ODR (Stolzy and Letey, 1962). The limiting water-film thickness is dependent on the soil porosity around the root and O_2 concentration in the pores. For example, a root cannot grow into the center of a saturated aggregate if its porosity is 30% and its diameter greater than 0.60 mm (assuming pore O_2 concentration is 21%). Calculations can be made on thin sections of soil aggregates to determine the fraction of the area that can allow root growth at various soil water contents and pore O_2 concentrations.

Fawcett (1936) attributed root rot of citrus to *Phytophthora citrophthora* (R. E. Sm. & E. H. Sm.) Leonian and *P. parasitica* Dast. The disease was favored by abundant soil moisture and was severe in clay soils where water drainage was impeded. Klotz *et al.*, (1971) found that parasitism by *Phytophthora* spp. was severe in well-aerated, but thoroughly watered, soil. Stolzy *et al.* (1965a) reported little or no decay of citrus feeder roots unless the soil was saturated (Table I). Several watering methods that enhanced root decay were developed by Stolzy *et al.* (1965b). Soil saturation was the key factor that increased root decay, and duration of saturation was more critical than frequency of saturation. Saturating the soil three times a month resulted in more root decay than saturating soil twice

TABLE I

Effects of Irrigation and O₂ Partial Pressure on Plant Growth, Root Decay, and Root-Tip Initiation in *Citrus sinensis*^a

Effects observed	Dry weight (per plant; g) ^b				Root decay (%)	New white root tips (number)
	Leaves	Stems	Roots	Total plant		
Irrigation ^c						
Control	2.14	1.42	1.86 _x	5.42	5 _w	
Water table	2.06	1.25	1.49 _{xy}	4.81	40 _x	
Saturated every 4 days	2.15	1.34	1.29 _y	4.77	52 _y	
Saturated 3 times a month	2.17	1.33	1.26 _y	4.75	65 _z	7
Saturated twice	2.15	1.37	1.65 _x	5.18	9 _w	15
Value	NS	NS	**	NS	**	NS
Aeration ^d (O ₂ partial pressure)						
Air (152 mm Hg)	2.48 _x	1.63 _x	2.50 _x	6.61 _x	8 _x	24 _x
N ₂ + air (10–13 mm Hg)	2.16 _y	1.32 _y	1.14 _y	4.61 _y	40 _y	3 _y
N ₂ gas (0.3 mm Hg)	1.76 _z	1.08 _y	0.90 _y	3.73 _z	55 _z	3 _y
F value	**	**	**	**	**	**
Coefficient of variability (%)	16	25	20	15	23	70

^aFrom Stolzy *et al.* (1965b).^bSubscript letters w, x, y, and z after mean values indicate statistical populations. Mean values are statistically significant only if they do not have a letter in common after values. NS, Differences of means not significant; **, F value significant at the 1% level.^cEach value is a mean of 12 internal replications.^dEach value is a mean of 20 internal replications.

a month, the latter a common practice among growers during summer months. Stolzy *et al.* (1965b) showed that low O₂ supply prevented growth and regeneration of citrus roots even in the absence of pathogens. Stolzy *et al.* (1967) studied root decay of avocado (*Persea americana* Mill. cv. Mexicola) in relation to O₂ diffusion, water regime, and *Phytophthora cinnamomi* Rands (Fig. 2). Significant root decay was found in saturated soils in the presence or absence of the fungus (Table II). The high water content also appeared to have an adverse effect on establishment of the fungus in the zoospore germ-tube stage. Oxygen deficiency in the root zone was the most important soil physical factor affecting growth and decay of roots. For plants growing in soils with O₂ diffusion rates of 0.17 μg cm⁻² min⁻¹, 44–100% of the root systems were in decay.

Saturated soils commonly occur in nursery and landscape plantings, which can predispose normally resistant rhododendrons to root and crown rot caused by *Phytophthora cinnamomi* (Blaker and MacDonald, 1981). Blaker and Mac-

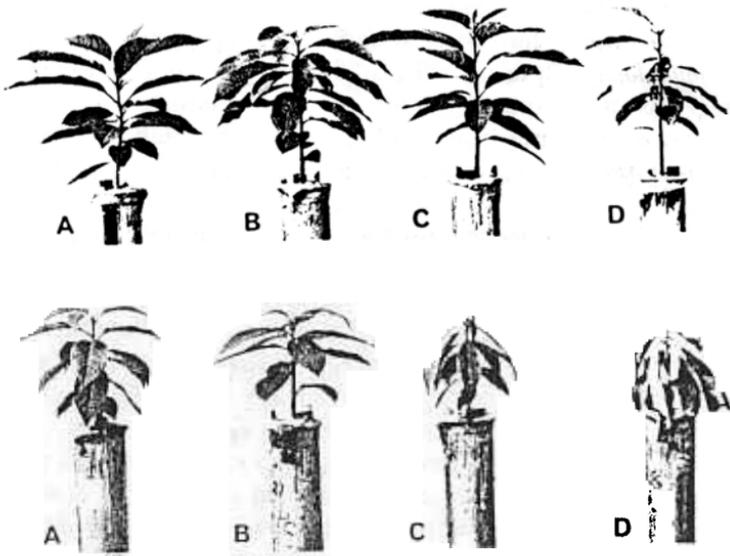


Fig. 2. One average plant from each treatment replication. The plants in the top row had O_2 concentration at the soil surface the same as that of air, whereas the bottom row had a reduced O_2 concentration at the surface. The letters refer to irrigation treatments: (A) control, (B) saturated every 10 days, (C) saturated every 4 days, and (D) water table. Soils were infested with a zoospore suspension of *Phytophthora cinnamomi*. From Stolzy *et al.* (1967).

Donald (1981) reported that root and crown rot of *Rhododendron* spp. was caused by *P. cinnamomi*. They subjected 1-year-old rhododendrons to various soil water regimes and inoculated them with motile zoospores of *P. cinnamomi*. In the absence of flooding, plants of the cultivar Purple Splendour developed severe root and crown rot following inoculation, whereas the cultivar Caroline remained free of symptoms and was relatively resistant. However, if Caroline roots were flooded for 48 hr before inoculation with *P. cinnamomi*, they developed severe symptoms of root and crown rot.

Armstrong (1981) listed four primary sequential stages of adaptive responses of higher plants to waterlogging: (1) soil waterlogging, (2) root O_2 stress, (3) decreased permeability of roots to water, and (4) plant water stress. Many of these effects were reviewed by Kozlowski (1976), Schoeneweiss (1975), Cannell (1977), and Levitt (1980). The effect of hormonal changes on plant response is an entire additional area of investigation of predisposing effects, but it also suggests the involvement of another important mechanism of plant adaptation, the release of root exudates (Fig. 3).

TABLE II

Effects of *Phytophthora cinnamomi*, Irrigation, and O₂ Supply on Plant Growth and Root Decay^a

Treatments	Dry weight (per plant; g)			Root decay (%)	Stage of disease ^b
	Shoots	Roots	Total		
<i>Phytophthora</i> ^c					
Absent	5.6	2.0	7.6	42	1.0
Present	5.1	2.0	6.9	55	1.4
Significance	*	NS	NS		
Irrigation ^d					
Check	5.4	2.0	7.4	39 _x	0.4 _x
Saturated every 10 days	5.1	1.9	6.7	46 _x	0.8 _x
Saturated every 4 days	5.8	2.1	7.9	37 _x	0.9 _x
Water table	5.0	1.9	7.0	72 _y	2.6 _y
Significance	NS	NS	NS	**	**
Aeration ^c					
High O ₂ supply	6.5	2.7	9.2	18	0.1
Low O ₂ supply	4.1	1.2	5.3	79	2.3
Significance	**	***	***	**	**
Interactions					
<i>Phytophthora</i> × irrigation	**	NS	*	NS	NS
Coefficient of variability (%)	19	25	20	44	32

^aFrom Stolzy *et al.* (1967).^bNumerical rating of plant tops as to the degree of root damage on a scale of 0 to 5 (0, healthy; 5, dead). Significance equals *F* value at level: *, 5%; **, 1%; ***, 0.1%. Subscript letters x and y after mean values indicate statistical populations. Mean values are statistically significant only if they do not have a letter in common after values.^cEach value is a mean of 32 internal replications.^dEach value is a mean of 15 internal replications.

B. Release of Exudates

Root exudates include soluble sugars, amino acids, organic acids, etc.; and insoluble substances, for example, cells and tissue fragments from root caps, epidermis, and cortex, polysaccharides, volatile compounds, etc. (Hale *et al.*, 1978). Virtually every soluble compound found in plants can be found in root exudates, depending on the plant species. Root exudation occurs as a result of certain environmental conditions, insects, nematodes, mechanical injury, and growth of secondary or lateral roots. The region of meristematic cells behind the root tip and the region of root elongation are sites of major exudation (Rovira and Davey, 1974).

Nematodes, fungi, and bacteria enter root tissues by penetrating the walls of the epidermis or through wounds (Balandreau and Knowles, 1978). Such inva-

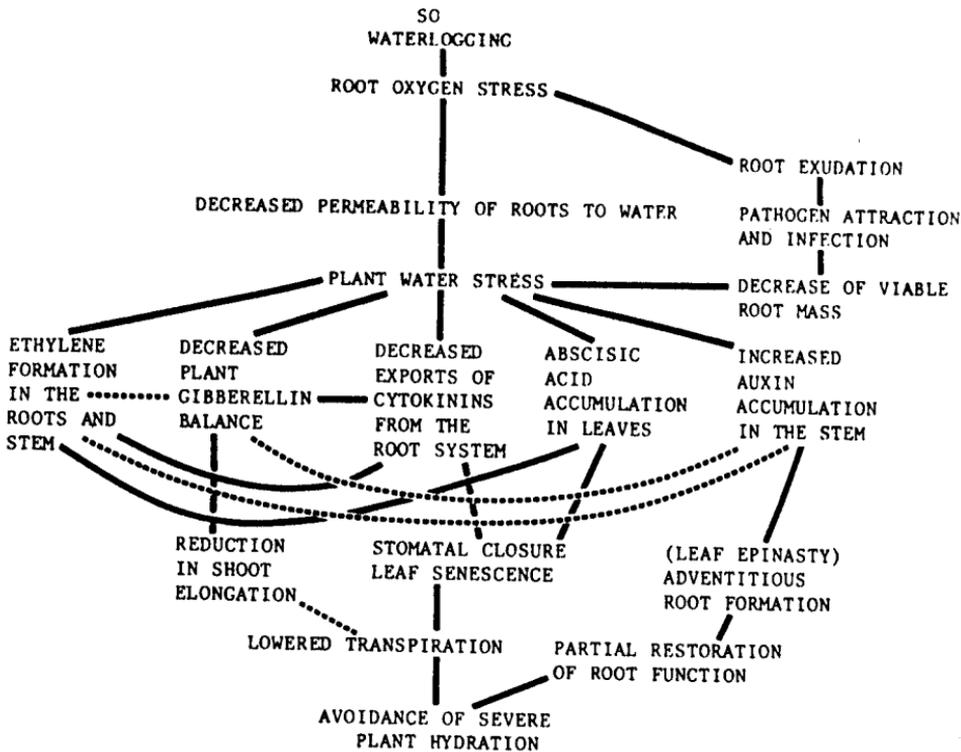


Fig. 3. Model showing the possible hormonal adaptive responses of higher plants to waterlogging stress. Unconfirmed interactions are represented by broken lines. Adapted from Armstrong (1981).

sion of roots affects the entire cortex of a living root, which provides invading microflora with a substrate equivalent to leaf litter, referred to as "root litter." Barber and Lynch (1977) supported the view that microorganisms stimulate the loss of soluble organic materials.

Hypoxia or anoxic conditions around the roots of flooded plants affect root exudation. Kuan and Erwin (1980) found lesions on the surface of alfalfa roots grown in soil saturated for 1 day. Also, the electrical conductivity of root exudate from the saturated soils increased from 15 to 22 mhos cm^{-1} , amino acids increased 30%, and sugar increased by 10% when compared to exudates from unsaturated soils. Labanauskas *et al.* (1974) measured amino acids in citrus leaves of plants growing in soils with normal and low soil- O_2 concentrations. The concentrations of the individual protein amino acids, the sum of individual protein amino acids, and percentage nitrogen in the leaves of low- O_2 plants were significantly lower than in leaves of plants grown with normal O_2 supply. Their study suggested a possible loss of amino acids from the plant to the soil under low soil O_2 . However, there is no direct evidence to substantiate this assumption.

Grineva (1961) found that soil anaerobiosis increased the dry weight of root exudates and the proportions of oxidizing compounds in corn (*Zea mays* L.) and sunflower (*Helianthus* sp.). Grineva concluded that cessation of aerobic respiration induced a shift in metabolism, resulting in secretion of nonmetabolized compounds, and induced formation and excretion of ethanol at the expense of sugar (Grineva, 1963). According to Hale *et al.* (1978), information is lacking on the effects of anoxia on root exudation. The effects of reduced O₂ on respiration are well known. Reduction in aerobic root respiration reduces energy available for maintenance of the active transport system. The permeability of cellular membranes changes and some substances leak out. The effects of exudates on plant diseases are discussed in Section VII.

V. FLOODING EFFECTS ON PLANT PATHOGENS

A. Fungi

1. Sporulation and Zoospore Release

Root-infecting microorganisms include fungi, bacteria, nematodes, and viruses. The list of diseases caused by fungi is extensive. Many are associated with flooded soil conditions. Diseases of root-infecting fungi may be divided into pathogen-dominant diseases and host-dominant diseases (Kommedahl and Windels, 1979).

Pathogen-dominant fungi are unspecialized pathogens that attack plants having little or no disease resistance; the pathogen is dominant over the host. Examples are *Rhizoctonia solani* Kühn, *Pythium* spp., and *Phytophthora* spp. *Rhizoctonia solani* is a complex pathogen that can damage plant roots or shoots in semiarid to aquatic environments. There are at least 66 known species of *Pythium* that are distributed in agricultural and undisturbed soils worldwide. They are pioneers in fungal ecological successions and are poor competitors for substrate. They form resting oospores when other fungi appear, accounting for their extended survival in soil in the absence of a host. *Phytophthora* and *Pythium* are closely related but differ in pathogenicity. *Phytophthora* causes disease on most plant parts, whereas *Pythium* is mainly a soil-inhabiting, root-infecting fungus (Kommedahl and Windels, 1979).

Host-dominant diseases involve pathogen-host associations in which the host has greater influence than the pathogen on the course of disease. Disease severity is greatest when the environment stresses the host for some time. Some examples of fungi causing host-dominant diseases are *Armillaria mellea* Vahl ex Fr., which causes root rot on hundreds of woody plants, *Fusarium* and *Verticillium*, which cause vascular wilt, and *Thielaviopsis basicola* (Berk. & Br.) Ferr., a soil-borne pathogen that causes root rot of more than 100 plant species.

Root exudates are essential for host-dominant diseases. Both groups of fungi

can persist in soil in an inactive state as resistant spores, sclerotia, or quiescent mycelia until activated by living roots (Curl, 1982). The influence of soil water on the reproductive structures of several *Phytophthora* species has been the subject of many studies. Soil water requirements for formation of sporangia in soil by *Phytophthora* are rather precise (MacDonald and Duniway, 1978a,b). The significance of ψ_m and osmotic ψ during the difficult developmental phases of selected mold oomycetes, including *Saprolegnia*, *Aphanomyces*, *Phythium*, and *Phytophthora* spp., was reviewed by Duniway (1979). Early studies recognized the association of saturated soil conditions with root decay. More precise methods for controlling ψ_m of soils have provided quantitative data on fungal water requirements. Duniway (1975b,c), MacDonald and Duniway, (1978a,b), Pfender *et al.* (1977), and Bernhardt and Grogan (1982) studied the formation of sporangia and release of zoospores by *Phytophthora cryptogea* Pethybr. & Laff, *P. megasperma* Drechs., *P. parasitica*, and *P. capsici* Leonian.

Gisi *et al.* (1979) studied production of sporangia by *Phytophthora cinnamomi* and *P. palmivora* (Butler) in sandy loam and clay soils at values of ψ_m between 0 and -15 bars. Number of sporangia produced was strongly correlated with ψ_m , but not with soil water content. Numbers of sporangia formed at a given ψ_m were similar for both soils. With buried mycelial inoculum, *P. cinnamomi* produced the most sporangia at -160 mbars with upper and lower limits between -10 and -250 mbars, whereas buried mycelial inoculum of *P. palmivora* produced the maximum numbers of sporangia in both soils at -10 mbars. Maximum numbers of sporangia were produced by *P. cinnamomi* on the soil surface only under flooded (1 mbar) and saturated (0 mbar) soil conditions. When washed mycelium or mycelial discs were used, the optimal ψ_m was between -10 and -100 mbars. When infected radicles (Pfender *et al.*, 1977) and infected leaf discs (Sugar, 1977) were used, the optimum was 0 mbar. The difference was attributed to inter- and intraspecific differences in sensitivity to aeration and/or water requirements.

It was suggested that the optimum ψ_m for infection from mycelial mats was different when infected tissue was used as inoculum. Kuan and Erwin (1982) showed that optimal ψ_m for sporangium formation on infected roots was 0 mbar compared to -100 mbars on mycelial discs. They suggested that infected roots provided a substrate for the fungus that differed from mycelial mats in its nutrient and water status and interaction with other microorganisms. Duniway (1983) and Sterne and McCarver (1980) reported that fewer sporangia formed at 0 than at -150 mbars ψ_m , but production of sporangia was similar at ψ_m between -25 and -150 mbars (Fig. 4). This was expected from the behavior of mycelial discs in soil. The important differences were that sporangia of *Phytophthora cryptogea* arising on roots formed more rapidly and in greater abundance and persisted longer than those produced on mycelial discs. The stage in the life cycle of *Phytophthora* most sensitive to flooding is during the release of zoospores from

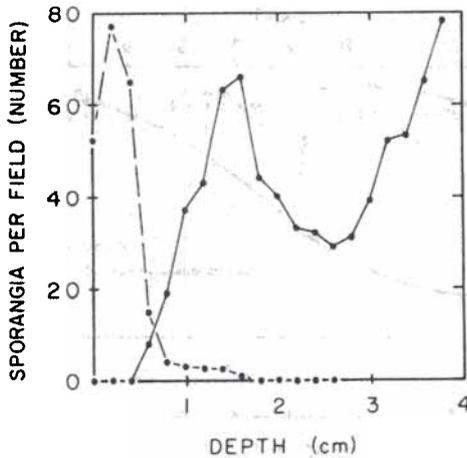


Fig. 4. Sporangium formation by *Phytophthora cryptogea* on roots of living safflower seedlings at various depths in soil maintained at ψ_m values of 0 (---) and -150 (—) mbars for 48 hr after inoculation. A microscope was used to count the sporangia in each field as one edge of a root was scanned from the level of the soil surface to the root tip. Representative data from 1 of 10 seedlings in each treatment are shown. From Duniway (1983).

sporangia (Duniway, 1979). The transition of soil from a drained to a saturated state stimulates zoospore release by sporangia. Prolonged flooding of soil helps in zoospore dispersal (Duniway, 1976). Many of the pathogenic host-dominant fungi infect roots by release of zoospores from sporangia.

Zoospore release occurs over a very narrow range of ψ_m near saturation. Indirect germination by release of zoospores may have a greater requirement for free water than does direct germination (Duniway, 1975a,c, 1979; Pfender *et al.*, 1977; Sugar, 1977; MacDonald and Duniway, 1978a,b).

Zoospore release from the sporangium of several species of *Phytophthora* can be divided into four intervals between swelling of the papilla: release of the second zoospore, rupture of the discharge vesicle, beginning of zoospore circling in the sporangium, and complete emptying of the sporangium (Gisi *et al.*, 1979; Gisi and Zentmyer, 1980). Most of the zoospore mass is forcibly expelled from the sporangium. The force of this cytoplasmic flow was attributed to changes in osmotic gradient and turgor pressure inside the sporangium (Gisi *et al.*, 1979).

2. Germination and Mobility

The effect of O_2 concentration on germination of zoospores of *Phytophthora parasitica*, *P. citrophthora*, and endoconidia of *Thielaviopsis basicola* was studied by Klotz *et al.* (1962, 1965). Liquid films around the zoospores were kept thin so O_2 diffusion for respiration would be high. The three fungi responded

differently to O₂ concentration by failure to germinate or by varying germ-tube lengths. These studies indicate the importance of O₂ supply on distribution of root-rotting fungi and, indirectly, on their parasitism of citrus roots. Zoospores of both *P. parasitica* and *P. citrophthora* germinated at very low O₂ concentrations, as would be the case in flooded soils. Zoospores of *T. basicola* germinated at a much higher O₂ concentration, more nearly resembling soil conditions at FC.

Phytophthora cinnamomi has been isolated from a wide range of soils and roots of plants (Hwang and Ko, 1978). The fungus produces sporangia on root surfaces, and chlamydozoospores in root tissues. Chlamydozoospores and oospores are believed to be the primary survival propagules of *P. parasitica* in soils. Tsao and Bricker (1968) demonstrated that a higher percentage of chlamydozoospores germinated in moist, nonsterile soils than in dry soils. Feld (1982) showed that chlamydozoospores of *P. parasitica* germinated more readily in soil with ψ_m between 0 and -50 mbars than in soil with ψ_m between -100 and -700 mbars. Germination of chlamydozoospores of *P. cinnamomi* in sandy loam soil was significantly lower at soil ψ_m of -250 mbars than at 0 to -10 mbars (Sterne *et al.*, 1977). However, when glucose and asparagine were added, germination increased in the drier soils.

Duniway (1976) determined that 100% of *Phytophthora cryptogea* sporangia were expelled within 1 day after the soil was saturated. MacDonald and Duniway (1978a) found that maximum germination of *P. megasperma* and *P. cryptogea* sporangia occurred when they were wetted to 0 mbar, with much less germination at -10 mbars and none at -25 mbars ψ_m . Zoospore release began ~1 hr after the soil was saturated and was nearly completed within 4 hr.

Several factors influence germination of oospores of *Phytophthora* spp., including light, sterols, temperature, maturity of the oospores, and the genetically controlled capacity of particular isolates to germinate (Zentmyer and Ervin, 1970). Light enhances germination of oospores of most *Phytophthora* spp. Soaking oospores of *P. megasperma* f. sp. *glycinea* in water for 48 hr increased their subsequent germination (Jimenez and Lockwood, 1981). Oospores germinated in flooded soil smears, soybean root exudates, and other substrates. Germination in natural or autoclaved soil was 50-60% compared with 10% in deionized water. Sporangia produced in unsterilized field soil seldom germinated.

B. Nematodes

1. Survival and Reproduction

Flooding soil for long periods has been used in attempting to control nematodes in field soils. This method, however, has usually been unsuccessful. McElroy (1967) observed that field populations of *Hemicycliophora arenaria* Raski were reduced in proportion to the frequency and duration of irrigation and postulated

that reduced aeration was the primary factor. Van Gundy *et al.* (1968) investigated ODR's in a flood-irrigated citrus orchard on sandy loam soil. Only a trace amount of dissolved O_2 was present to a 61-cm depth immediately following irrigation. After 12 hr, O_2 had diffused to a depth of 15 cm, but 7 days were required for restoration of normal ODR's to the entire soil depth. A profile of the ODR's following irrigation was determined (Fig. 5). Even short-duration irrigations slowed nematode reproduction. In this study, O_2 supply dropped to low levels during flood irrigation and gradually rose following water application, requiring 7–9 days for normal O_2 levels to return to a depth of 61 cm. Therefore, a large part of the soil profile, between 15 and 61 cm, experienced microaerobic conditions ($<5\% O_2$) for several days. When irrigation frequency increased during summer months, the duration of adequate soil aeration periods for nematodes decreased, and at depths of 30–61 cm, nematodes were continuously exposed to low levels of O_2 . Continuous aeration of the surface soil horizon, however, could maintain nematode populations. Such is not the case in many agricultural soils, however,

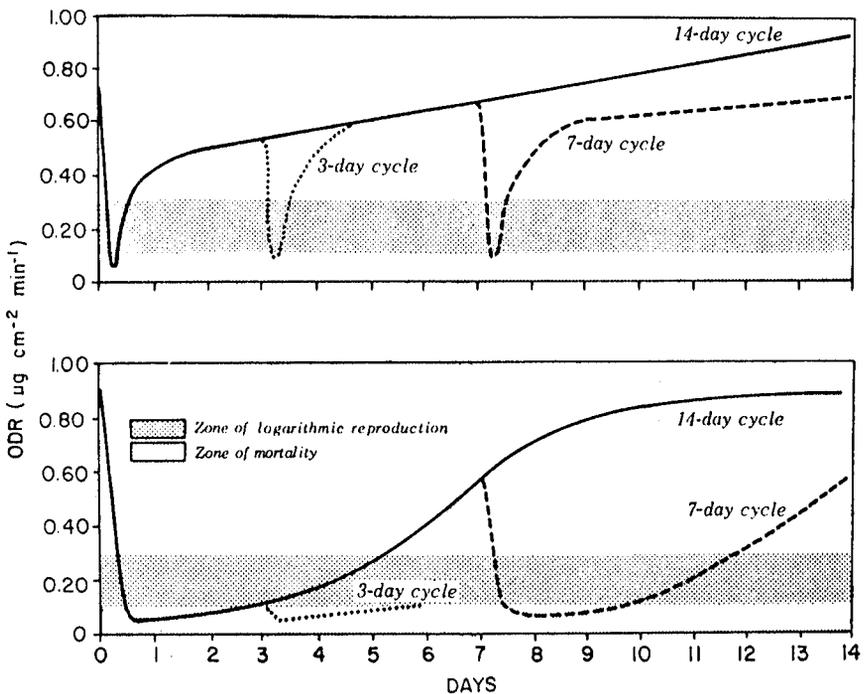


Fig. 5. A diagrammatic presentation of the relationship of the frequency of irrigation of ODR and to nematode mortality and reproduction at 12-in. (top) and 24-in. (bottom) depths. From Van Gundy *et al.* (1968). Copyright 1968 The Williams and Wilkins Co., Baltimore.

because tillage, partial drying, and high temperature in the surface horizon are not conducive to nematode growth and reproduction.

Oxygen in the soil atmosphere depends on the rate of diffusion in the gaseous phase. The most important factor controlling gaseous diffusion is the soil ψ_m . Furthermore, O_2 diffusion into water-saturated soil aggregates is not controlled by gas-filled macropore spaces, but by the water-filled micropores of the aggregates (Stolzy *et al.*, 1981). Because of their size, egg sacs and larvae of nematodes are found in these aggregates and are subjected to wide fluctuations in aeration. Both the hatch and mobility of *Meloidogyne javanica* (Treub) Chitwood are low when the pore spaces are filled with water (Wallace 1968b). Van Gundy and Stolzy (1961) showed that the lowest O_2 concentration that allowed development of the host and the nematode was 3.5%. Also, there was a linear relationship between movement of *M. javanica* larvae and the rate of O_2 diffusion in a porous medium (Van Gundy and Stolzy, 1963).

Cooper *et al.* (1970) pointed out that the study of nematodes in controlled environments involves constant conditions that are easily controlled (Overgaard-Nielsen, 1949; Feder and Feldmesser, 1955; Wallace, 1956; Feldmesser *et al.*, 1958; Fairbairn, 1960; Nicholas and Jantunen, 1964, 1966). Their data indicate that this general group of nematodes consists of facultative anaerobes: growth and reproduction are dependent on a sufficient supply of O_2 , but they can survive anaerobic conditions for varying periods. Soil-inhabiting nematodes are adapted to the changes in soil aeration. However, aeration increases in importance for nematode survival under irrigation and in high-rainfall areas.

Reproduction of a wide variety of soil-inhabiting nematodes is severely reduced in continuously microaerobic environments (Fairbairn, 1960; Nicholas and Jantunen, 1966; Bryant *et al.*, 1967; Saz, 1969). The rate of reproduction of *Aphelenchus avenae* Bastian, *Hemicycliophora arenaria*, and *Caenorhabditis* sp. was significantly decreased in a continuous environment of 5% O_2 and was inhibited at 4% (Cooper *et al.*, 1970). The physiological processes essential for reproduction and growth are apparently aerobic. Many researchers have assumed that short interruptions of O_2 are of little consequence to nematodes. However, Cooper *et al.* (1970) found that short-interval fluctuations between high and low O_2 can also be highly disruptive to nematode survival and reproduction. The closer the interval between the high and low O_2 concentrations, the greater influence on population number. Conversely, the longer the interval, the less the influence. Van Gundy *et al.* (1968) also showed that longer intervals between applications of irrigation water maintained larger nematode populations. Two of the nematodes (*A. avenae* and *Caenorhabditis* sp.) are capable of performing anaerobic glycolysis in microaerobic (<5% O_2) and anaerobic environments and easily survive short exposures to low O_2 levels (Cooper and Van Gundy, 1970). The shunting back and forth between oxidative and fermentative metabolism prevents nematodes from developing an adequate capacity for continuous ana-

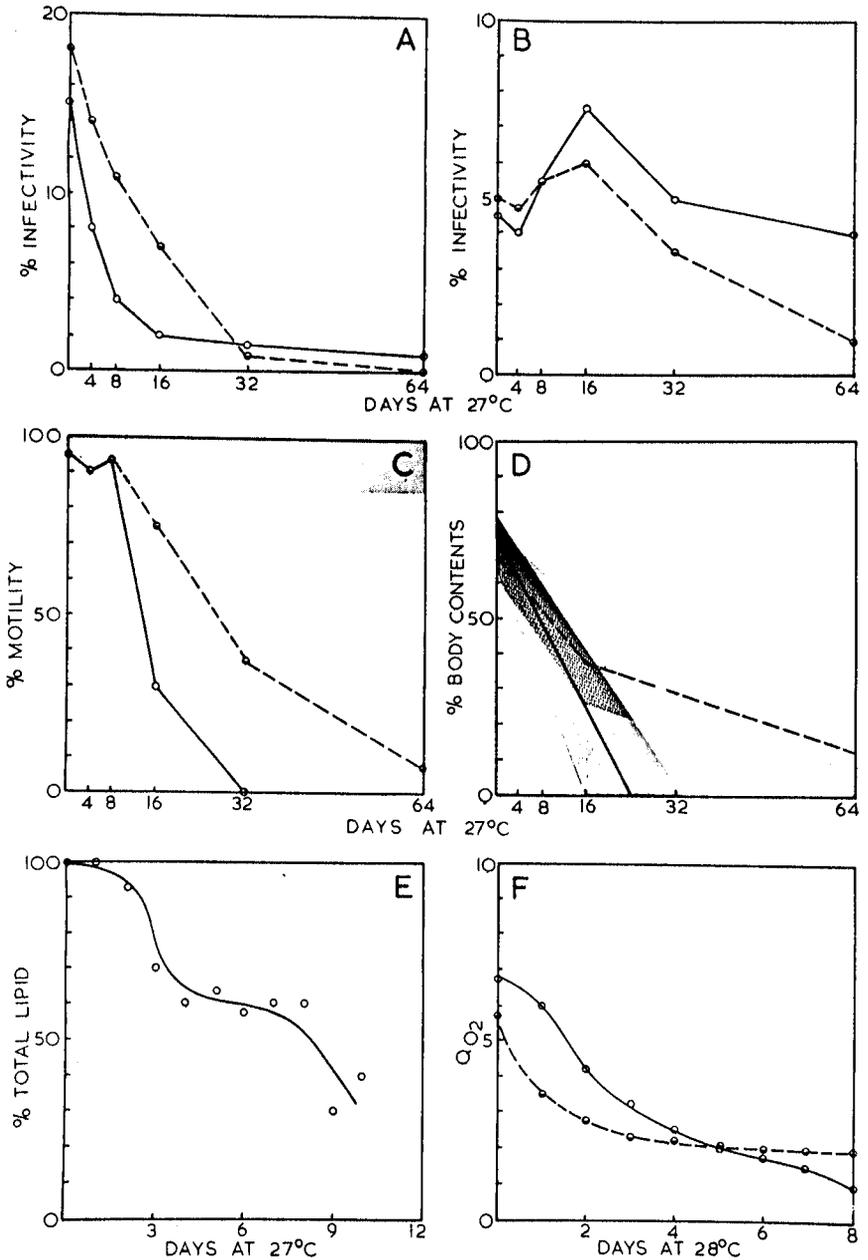


Fig. 6. (A) Mean percentages of *Meliodogyne javanica* larvae developing into adults on tomato and citrus seedlings, after being stored at 27°C *in vitro* (- -) and in soil (—). (B) Mean percentages of *Tylenchulus semipenetrans* larvae developing into adults on citrus seedlings after being stored at 27°C

bolism and interferes with such processes as lipid metabolism in egg production, egg hatch, etc. Van Gundy and Stolzy (1961, 1963) observed that females of *H. arenaria*, *M. javanica*, and *Tylenchulus semipenetrans* Cobb did not lay as many eggs in continuously microaerobic environments as they did in continuously aerobic ones. Le Jambre and Whitlock (1967) reported similar results for some animal-parasitic nematodes. Behavioral responses to physiological stimuli caused by fluctuating environments affect the egg-laying stage in the life cycle.

During the first 12–16 hr of exposure to microaerobic and anaerobic environments, the principal glycolytic end product of *Aphelenchus avenae* and *Caenorhabditis* spp. was lactic acid. After 16 hr it was ethanol (Cooper and Van Gundy, 1971). On return to aerobiosis, [¹⁴C]ethanol in the medium was utilized by the nematodes.

Wallace (1968b) showed a linear relationship between O₂ concentration and hatch rate of *Meloidogyne javanica*. Hatching did not occur in the absence of O₂. After 2 days without O₂, there was a marked decrease in hatch because of susceptibility of embryonated eggs to anaerobic conditions. Wallace concluded that low O₂ resulting from waterlogging or soil depth may have a contrasting dual effect; it may kill embryos, but it may also maintain infectivity in larvae by inducing quiescence. Van Gundy *et al.* (1967) showed that a decrease in infectivity was associated with a corresponding decrease in mobility and body contents of second-stage larvae of *M. javanica* and *Tylenchulus semipenetrans* that were aged and starved in soil (Fig. 6). Body contents were consumed rapidly at high temperatures in dry soils and in oxygenated solutions. Conversely, body contents were conserved and motility and infectivity increased at low temperatures in wet soils and in low-O₂ solutions. Their observations explain why flooding of soils does not eradicate nematodes. Flooding in most agricultural soils does not produce completely anaerobic environments.

2. Mobility

Wallace (1968a) reviewed how nematodes, particularly plant-parasitic species, move in the various environments encountered during their life cycle. In most cases, nematodes move by undulatory propulsion, in which a train of dorsoventral waves passes from the head to tail. Because of their morphological

in vitro (---) and in soil (—). (C–F) —, *Meloidogyne javanica*; ---, *Tylenchulus semipenetrans*. (C) Mean percentages of larvae stored *in vitro* that migrated through a 1-cm sand column after 3 hr. Values within the shaded area are not statistically different ($p = 1\%$). (D) Mean percentages of body contents of larvae stored *in vitro*. The maximum variation of individuals in four experiments is represented by the shaded area for each nematode. The LSD between means is 3.37%. (E) Percentage loss of total lipid in *M. javanica* larvae when aged in shaking Warburg flasks at 27°C. (F) Mean respiration rates ($\mu\text{l O}_2 \text{ mg}^{-1} \text{ hr}^{-1}$) of nematodes aged in a shaking Warburg flask at 28°C. From Van Gundy *et al.* (1967).

simplicity and lack of appendages, nematodes exert a force against external objects in *one* direction by undulatory propulsion. This mechanism is similar in all environments. The speed of larval migration and nematode hatch rate have the same relation to ψ_m (Collis-George and Wallace, 1968). In saturated or dry soil, the rate of hatch is low and migration of larvae low or negligible. When soil pores are filled with water, the nematodes are not attracted to soil particles because of water-film thickness. In dry soil, water films are thin and nematodes are tightly restricted to a small volume near the soil particles. As soil water content decreases from saturation to FC, the soil environment is most conducive to egg hatch, rapid migration of nematodes, and quick invasion of a host root.

VI. DISSEMINATION OF PATHOGENS BY FLOODING

A. Lateral Dispersal on the Soil Surface

Phytophthora citrophthora, *P. parasitica*, *P. syringae* Kleb, *P. hibernalis* Carne, and *P. megasperma* are pathogenic either to above- or below-ground tissues of commercially grown citrus in California. Klotz *et al.* (1959) extensively surveyed various surface water sources throughout the state over a year-long period and found that zoospores of *Phytophthora* spp. were effectively dispersed, both actively and passively, in all surface waters. Temperature and season affected the species prevalent at the time of sampling.

Southern Georgia is a major producer of certified vegetable and ornamental transplants for shipment to other areas. Fumigants are used to control soilborne plant pathogens (Shokes and McCarter, 1979). However, reinfestation of fumigated fields has limited the success of the control program. Transplants are irrigated with sprinkler systems drawing water from ponds that receive runoff from surrounding fields. Shokes and McCarter (1979) listed numerous studies conducted in many areas of the United States where pathogens were present in irrigation waters. Few of these studies show how these pathogens are disseminated or what their survival rate is in pond waters. Ponds were sampled regularly in southern Georgia for plant pathogens and at different depths and locations in the ponds as well as from filtered debris and bottom sediments. Plant-pathogenic fungi from samples included more than 20 species of *Pythium*, *Phytophthora*, *Fusarium*, and *Rhizoctonia*. One sample taken by filtering water from an irrigation line in the field yielded 5 *Pythium* species, 1 *Phytophthora* species, and 14 lance nematodes. Oospores of *Pythium aphanidermatum* (Edson) Fitzp. were recoverable for 185 days after submersion in a pond, whereas zoospores were not recovered after 12 days. Frequent sprinkler irrigation increased the incidence of avocado root rot (Zentmyer and Richards, 1952).

Hickman and English (1951) found that saturated soils with moving water were necessary to move zoospores of *Phytophthora fragariae* Hickman to the host, whereas excessive water in soybean [*Glycine max* (L.) Merr.] fields in-

creased recovery of *P. megasperma* var. *sojae*, the amount of zoospore inoculum in runoff water, and incidence of disease (Kein, 1959). McIntosh (1964, 1966) detected *Phytophthora* spp. parasitic to apples (*Pyrus malus* L.) in irrigation waters.

B. Vertical Movement in the Soil

The movement of fungal zoospores vertically through soil profiles depends on soil-water conditions. Zoospores of *Phytophthora* spp. swim in a helical pattern (Ho and Hickman, 1967a,b; Hickman, 1970; Allen and Newhook, 1973). Stolzy *et al.* (1965b) calculated that soil pores with diameters between 40 and 60 μm are necessary to accommodate this type of motion of the zoospores with flagella extended. Water-filled pores of smaller diameter would lead to spore encystment when zoospores collided with soil particles. Soil pores of $\sim 300 \mu\text{m}$ in diameter drain water at soil ψ_m of -10 mbars (Cook and Papendick, 1972; Griffin, 1972, Duniway, 1976). Chemotaxic and passive zoospore movements in soil generally occur only when soil ψ_m is higher than -10 mbars. Zoospore movement apparently requires continuous water-filled channels with a minimum of tortuosity. Movement of *P. cryptogea* zoospores in a coarse-textured soil mix was reduced at -100 mbars ψ_m , and in a finer loam, movement was reduced at -10 mbars. Duniway (1976, 1979) suggested that water-filled channels greater than 60 μm in diameter are required for prolonged zoospore movement. Duniway showed that zoospores readily swam 25–35 mm in the surface water over flooded soils or through coarse-textured soils with ψ_m of -0.5 mbar (Fig. 7).

Phytophthora megasperma zoospores and cysts and *Serratia marcescens* Bizio cells were infiltrated from the outflow of horizontal soil columns during the establishment of a gradient of ψ_m (Wilkinson *et al.* 1981). In soil columns wetted a distance of 65 cm, zoospores moved 35 cm behind the wetting front in sand, 44 cm in sandy clay loam, 48 cm in loam, and did not move in silty loam soil. The soil ψ_m at the boundary between infested and noninfested soils ranged from -14 to -18 mbars. Zoospore cysts moved only half the distance that motile zoospores moved, whereas *S. marcescens* cells were recovered close behind the wetting front. The data of Wilkinson *et al.* indicate that infiltration of propagules occurred after soil pores with radii considerably larger than a priori estimates of the limiting pore radii were filled with water.

Pfender *et al.* (1977) found that zoospores originating from sporangia produced at various depths in two flooded soils were detected in surface water. Zoospores migrated upward through 65 mm of a sandy loam soil, but rarely moved 24 mm upward through a silt loam soil. In the flooded silt loam, the probability that zoospores would reach the ponded water at the soil surface depended on the number of sporangia and their depth in the soil.

The rate of active movement of five isolates of soil bacteria was measured in natural and artificial soils at a soil ψ_m of -50 and -150 mbars (Wong and

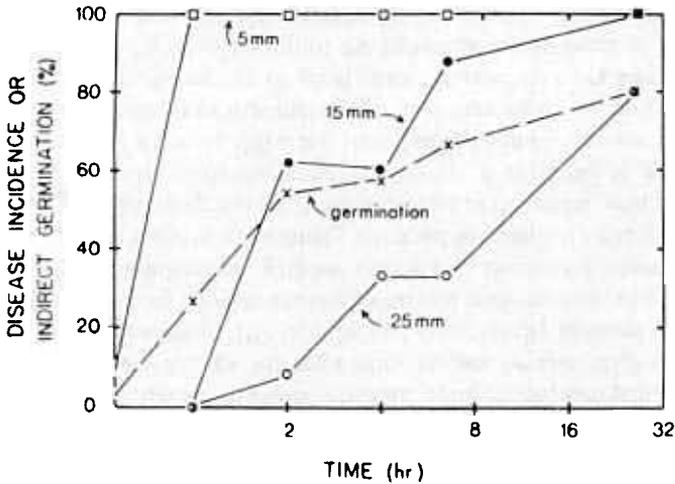


Fig. 7. Influence of the distance from sporangia on the rate at which *Phytophthora cryptogea* infected susceptible safflower seedlings when a coarse-textured soil mix was saturated. The soil was saturated to $\psi_m = 0$ without flooding at time zero, and tension plates were periodically used to drain the soil and stop indirect germination and zoospore movement. From Duniway (1983).

Griffin, 1976). At the same soil ψ_m , all organisms moved faster in the artificial soil was attributed to fewer surface charges to which bacteria became adsorbed. The studies concluded that bacterial movement is restricted in soil drier than FC. Generally, the distance of movement of microbial cells in the soil depends on adsorption of the cells on the soil solid phase, on water content, and on rate of water flow (Bitton *et al.*, 1974). Britton *et al.* found that passive infiltration of bacterial cells into dry soil columns was affected by soil type and that their upward movement stopped when the water content was at or below FC.

VII. ROOT-PATHOGEN INTERACTIONS

A. Root Attraction

The "rhizosphere effect" (Fig. 8) refers to the chemical or physical influence of living roots on microbial activity and the results of this activity on plant health and vigor (Curl, 1982). Root exudates are the primary contributing factor. Studies have shown that components of root exudates directly affect propagule germination, mycelial growth, and reproduction of pathogens.

Zoospores of the plant pathogenic fungi *Pythium* and *Phytophthora* are attracted to roots and to exudates from roots. Zoospore accumulation on roots is influenced by attraction, trapping, rapid encystment and germination, morphogenetic origin of zoospores, and directed growth of germ tubes (Hickman and Ho, 1966).

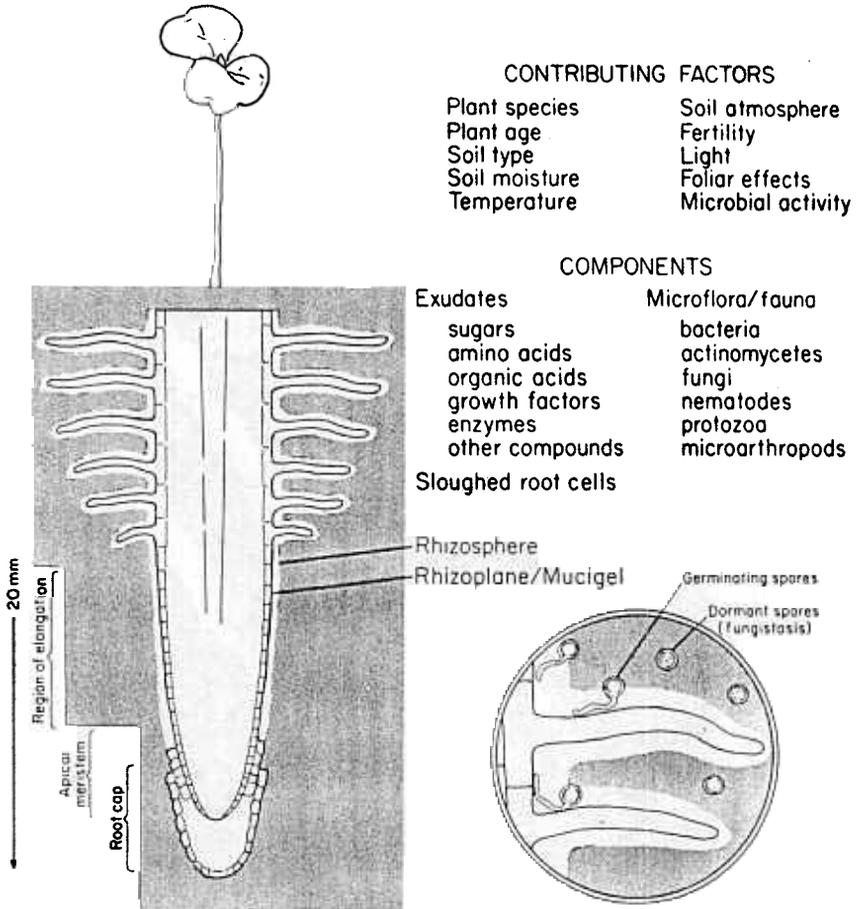


Fig. 8. Diagrammatic representation of the rhizosphere of a small cotton root, with lists of exudate and microbial components and influencing factors. Fungal spores within the rhizosphere (round inset) are stimulated to germinate. From Curl (1982).

According to Cameron and Carlisle (1978), zoospore attraction (positive chemotaxis) to amino acids, which occur in root exudates, and to ethanol produced by roots in waterlogged soils has been demonstrated. However, no single specific substance appears to be as strong an attractant as actual root exudate. Cameron and Carlisle (1978) emphasized that attractiveness of root exudates must be explained by additive or multiplicative effects between individual attractants or by powerful attractants that have not yet been detected, or both. Zentmyer (1961) confirmed that *Phytophthora palmivora* zoospores were attracted to certain amino acids and responded, as did *P. cinnamomi* zoospores, to ethanol. Allen and Newhook (1973) found that *P. cinnamomi* showed chemotaxis to

solutions of methanol, *n*-propanol, *n*-butanol, and acetaldehyde. Cameron and Carlisle (1978), however, found that *P. palmivora* was attracted only to acetylaldehyde in the aforementioned chemical solutions. Several alcohols, aldehydes, and fatty acids also served as attractants, with thresholds considerably lower than those for ethanol. The most potent attractants had 4–6 carbon atoms, and iso compounds tended to be more effective than those with straight chains. Zoospores of *P. palmivora* and *P. cinnamomi* were repelled by H^+ and other monovalent ions.

Kuan and Erwin (1980) demonstrated that roots of plants grown in saturated soil attracted many more zoospores than did roots from plants in unsaturated soil. Zoospores were chemotactically attracted preferentially to the zone of cell elongation and to tissue from which secondary roots emerged (Fig. 9). More sugars and amino acids were found in exudate from roots grown in saturated soils than in exudates of roots grown in unsaturated soil. Zentmyer (1966) concluded that zoospores of *Phytophthora cinnamomi* were attracted to glutamic acid and aspartic acid and those of *P. palmivora* and *P. citrophthora* to glutamic acid, aspartic acid, asparagine, glycine, methionine, histidine, glutaric acid, and to several sugars.

The region of cell elongation of roots appears to produce more exudates and to attract more zoospores than other root tissues. Chi and Sabo (1978) showed that zoospores were strongly attracted to the region of cell elongation, immediately above the root cap or older regions of the roots, and none were attracted to root hairs in their study. This study also showed that susceptible seedlings of alfalfa roots pretreated in boiling water did not attract zoospores. Wounded parts of roots displayed a strong preferential attraction for zoospores. These responses were attributed to chemotaxis associated with chemicals in root exudates.

Zoospores of five species of *Phytophthora* responded positively to a wide range of chemicals, including vitamins, phenolic compounds, nitrogenous bases of nucleic acids, nucleotides, growth regulators, sugars, organic acids, and amino acids (Khew and Zentmyer, 1973); a distinct directionally oriented attraction to amino acids was noted. Several chemicals caused accumulation of zoospores by trapping and immobilization without evoking a directional movement of zoospores. Zoospores were more strongly attracted to positively charged molecules than to negatively charged ones. Ionic structure of the amino acid molecule is important in determining its chemotactic activity. A response to a possible concentration gradient of some diffusing stimulatory chemical in root exudates was demonstrated by zoospores that had encysted at varying distances from avocado roots. Positive chemotropism of germ tubes for avocado roots was reported when zoospores settled on the bottom of the petri dish at distances of 2–3 mm from the root and then grew unidirectionally toward the root. However, ethanol in isotropic solutions did not affect the average speed, velocity, amplitude, frequency of the helical path, or rate of change of direction of zoospores of *P.*



Fig. 9. Attraction of zoospores of *Phytophthora megasperma* f. sp. *medicaginis* to alfalfa roots grown in saturated (S) and nonsaturated (NS) soil. Area between arrows is the zone of encysted zoospores. From Kuan and Erwin (1980).

cinnamomi. When moving through concentration gradients of ethanol, however, zoospores turned, moved to the higher concentration, and accumulated in numbers (Allen and Newhook, 1973). In the absence of ethanol, zoospores entering capillaries were disoriented, but zoospores germinated in gradients of ethanol had their germ tubes directed toward the source. Ethanol production by plant roots during brief periods of low soil aeration after flooding attracted zoospores to its site of exudation.

Zoospores of two *Pythium* species were attracted to the region of cell elongation of roots of cotton (*Gossypium hirsutum* L.) seedlings as well as to root-hair zones (Spencer and Cooper, 1967). Wounds in radicles greatly intensified the attraction.

Bird's (1962) experiments on orientation of *Meloidogyne javanica* larvae toward roots supported the root-attraction hypothesis. Bird concluded that attraction of larvae to roots is the result of several stimuli and not merely to CO₂ in the vicinity of roots, as had been suggested by several other investigators.

B. Root Infection by Zoospores

Zoospores of *Phytophthora megasperma* var. *sojae* were attracted to the root and then trapped in the vicinity of the root surface, after which they encysted in less than 1 hr (Ho and Hickman, 1967a,b; Chi and Sabo, 1978). The encysted zoospores formed a continuous sheath around the root behind the tip, and then germinated. Germ tubes were initiated on the cysts closest to the root, and all showed unidirectional growth toward the root. *Pythium* species penetrate and infect cotton-seedling radicles by germ tubes from single zoospores. These zoospores, as well as single mycelial tips, were attracted in aqueous media to plant roots (Spencer and Cooper, 1967). Infection of root radicles by a germ tube from single zoospores occurred within 2 hr and by single mycelial tips after the much longer time of 12 hr.

Studies by Klotz *et al.* (1962, 1963) on germination and germ-tube growth of zoospores of *Phytophthora* spp. and *Thielaviopsis basicola* showed that after swarming, *Phytophthora* spp. took only 1.5 hr to germinate even at low O₂ levels, whereas *T. basicola* took 7 hr at much higher O₂ concentrations.

In flooded fields, zoospores are generally the initial inoculant, as they are carried by moving water to plants in noninfested areas. Severity of root rot of avocado caused by *Phytophthora cinnamomi* increased when the water content of soil remained near saturation because of overirrigation or poor drainage (Zentmyer *et al.*, 1967). Disease severity on peach trees induced by *Pythium vexans* d. By. was correlated with an increase in zoospore production as a result of periodic excess water (Biesbrock and Hendrix, 1970). Encysted zoospores of *Phytophthora megasperma* on alfalfa roots germinated, and the germ tubes grew

toward breaks in the roots caused by saturated soil conditions (Kuan and Irwin, 1980). Bacteria as well as germinated zoospores occupied the breaks on roots grown in saturated soil.

Root pathogens may damage the host primarily by decreasing effective root density and distribution of roots in the soil, thereby lessening the capacity of plants to extract water and nutrients from soil (Duniway, 1977a). The interrelationships of root-rotting fungi, soil O_2 , and saturated soil were discussed by Stolzy *et al.* (1960, 1965b). Saturated soils limit soil aeration. Many orchards are saturated to different depths for a period of time after an irrigation. Root survival in a saturated zone depends on the drainage characteristics of the soil profile. If water moves out of the profile rapidly and O_2 is soon available, growth of older roots and regeneration of new roots will start soon after irrigation stops. If the water drains away slowly, root density will decrease with time. Good irrigation practices on poorly drained soils are more critical than on well-drained soils. The amount of irrigation water added at any time should be based on the amount needed to rewet the dry surface soil without saturating the subsoil. Orchards on coarse-textured soils, such as loamy sands and sands, lack feeder roots in the surface 1 m of profile between tree rows where water is applied. Water infiltration into and through the soil profiles is rapid because of large continuous pore spaces. The absence of feeder roots is the result of parasitism by zoospores produced at the soil surface that have moved to root surfaces in water. The running water at the soil surface is ideal for production of zoospores. The range of soil ψ_m that would drain soil pores between 40 and 60 μm would be -24 to -36 mbars, potentials achieved in these soils during furrow irrigation.

Feld (1982) conducted furrow- and drip-irrigation studies under controlled conditions in a lath house and greenhouse. Citrus root rot caused by *Phytophthora parasitica* was favored by overirrigated soil under furrow irrigation when soil ψ_m was between -0 and -150 mbars, and consistently moist soil under drip irrigation between -50 and -300 mbars. Very few new feeder root tips were produced by roots growing in soil under these two irrigation treatments. Feld (1982) showed that where citrus was grown under a furrow-irrigation system, and the soil was allowed to dry sufficiently between irrigations (to -700 mbars), new feeder roots were continually produced and plants were healthier than those allowed to dry to only -150 mbars or kept wet by drip irrigation.

Stolzy *et al.* (1959) flood-irrigated citrus seedlings growing in loamy fine sand contained in large concrete tiles with and without *Phytophthora* spp. Irrigation treatments consisted of watering the entire 1-m soil columns at values of soil ψ_m of -90 or -600 mbars. The amount of water added at each irrigation lowered the ψ_m at the bottom of the column to -20 mbars. Saturation of soil occurred only at the top of the soil column during irrigations. The -90 -mbar treatment produced more total plant growth during 2 years, in both the presence and

absence of the fungi, than did the dry treatments. However, presence of *Phytophthora* significantly reduced shoot and root growth. This and other experiments demonstrated that by proper management of irrigation waters, to prevent soil saturation in the profile, plants in hot, dry environments yielded more when watered at a high ψ_m (Stolzy *et al.*, 1959, 1960, 1965b; Lombard *et al.*, 1965).

VIII PLANT WATER STRESS AS A PREDISPOSING FACTOR

Variations in precipitation and irrigation frequency differentially influence water balance in plants, often causing many adverse effects. One such effect is an increase in susceptibility of plants to attack by plant pathogens (Schoeneweiss, 1978). When the susceptibility of the plant is altered before an infection, the plant is predisposed to disease. The most common method of exposing plants to water stress is by varying watering regimes. For example, drought may enhance disease development in the plant following irrigation because of water-stress predisposition. Duniway (1977b) withheld water from safflower plants until leaf ψ was -13 or -17 bars before inoculation with zoospores of *Phytophthora cryptogea*. This treatment increased root rot by the fungi when compared to plants watered daily when leaf ψ was between -4 and -6 bars. With the exception of saturated soils, various soil water regimes after inoculation were almost equally suitable for development of severe root rot. Depending on methods used, saturated soil was more or less suitable than drier soil for disease development. Also, Zimmer and Urie (1967) demonstrated that irrigation frequency and intensity influenced root rot of safflower varieties grown in infected fields. Some varieties were killed by all irrigation treatments, whereas others were only slightly or moderately affected under frequent light irrigations and severely affected under prolonged irrigation. Water stress prior to irrigation increased the incidence of root rot.

Severity of alfalfa root rot in the seeding year increased through a combination of stress factors, including high soil-water levels, frequent cutting, high seeding rates, and late spring seeding (Pulli and Tesar, 1975).

The rhododendron cultivar Caroline was relatively resistant to crown rot of *Phytophthora cinnamomi* (Blaker and MacDonald, 1981). However, if plants were exposed to drought until leaf ψ dropped to -16 bars, or if their roots were flooded for 48 hr before inoculation with fungi, they developed severe symptoms of root and crown rot. Blaker and MacDonald's data showed that soil water extremes that commonly occur in nursery or landscape plantings can predispose normally resistant rhododendrons to root and crown rot. An understanding of how the host resists attack by a pathogen is necessary to determine how water stress causes a plant to become predisposed to disease (Schoeneweiss, 1978).

IX CONTROL OF DISEASE BY FLOODING

Mulder (1979) and Schippers and Gams (1979) discussed soil management for control of soilborne pathogens. Their reviews indicate that nearly all aspects of soil management and soil-intrinsic properties may have a measurable impact on pathogen virulence. Such properties include soil texture, mineralogy, organic and biological composition, nutrient availability and other chemical effects, crop rotation, tillage practices, crop-residue management, soil temperature, soil ODR, and flooding. Infection and development of disease in plants can be reduced by changes in soil resulting from waterlogging. The waterlogged soil environment is more favorable to microorganisms antagonistic to plant pathogens than at FC (Drew and Lynch, 1980). Stover (1979) reviewed the flooding of soil for disease control.

Ioannou *et al.* (1977a,c) studied production of microsclerotia in tomato [*Lycopersicon esculentum* (L.) Mill.] tissues infested with *Verticillium dahliae* Kleb. in soil subjected to different water treatments under field conditions. Equal numbers of microsclerotia were produced in dry or one-irrigation treatments, but none were produced during flooding. The inhibition of microsclerotia production was due in large part to decreased O₂ and increased CO₂ concentrations in the flooded soil. In another study, Ioannou *et al.* (1977b) showed that production of microsclerotia was completely inhibited at concentrations of 10% O₂ and 11% CO₂ in the soil.

A single rotation with paddy rice (*Oryza sativa* L.) controlled *Verticillium* wilt of cotton for 2–3 years and increased lint yield by an average of 31% over 3 years when compared to areas in which cotton was continuously grown (Pullman and DeVay, 1981). Four years after the single rice rotation, soil populations of *V. dahliae* were still much lower than the initial populations. Six weeks of soil flooding with or without rice was required before population densities began to decline. However, after 17 weeks of flooding in the presence of paddy rice, *V. dahliae* was not detectable, whereas with flooding alone 9% of the initial population was still present.

• Fungi are favored by a relatively dry environment and bacteria by wet conditions (Cook and Papendick, 1972). Stover (1979) reported that only one species of bacteria, *Pseudomonas solanacearum*, on tobacco (*Nicotiana*) and bananas (*Musa*) was controlled by flooding. The lower fungi are an exception and require more water for zoospore movement. Excessive soil water is often harmful to higher fungi, and waterlogging could eliminate some sensitive species (Mangenot and Diem, 1979). Stover (1979) pointed out that numerous practices used in long-term flooding helped control various pathogens. Because sufficient O₂ is available in the surface few millimeters of ponded or waterlogged soil to sustain organisms during flooding, the use of interflood deep plowing or postflood application of fungicide enhance control. Certain pathogens are more effectively

controlled by alternating short-term flooding and drying. And, finally, because of the higher demand for O_2 by respiring microorganisms at high temperatures, pathogens can be better controlled by flooding when soil temperatures are high than when they are low. If crops are present during flooding, high soil temperatures during flooding will also cause O_2 stress to roots as well as to microorganisms.

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