Effect of Dissolved Oxygen Concentration on the Relative Susceptibility of Shortleaf and Loblolly Pine Root Tips to *Phytophthora cinnamomi*

S. W. Fraedrich and F. H. Tainter

Former graduate research assistant and professor, respectively, Department of Forestry, Clemson University, Clemson, SC 29634-1003; Present address of first author: Forestry Sciences Laboratory, USDA Forest Service, P. O. Box 70, Olustee, FL 32072.
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ABSTRACT

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Exposure of shortleaf and loblolly pine lateral roots to oxygen concentrations of 0–0.25 mg/L for durations of 6–24 hr before inoculation increased root susceptibility to infection by *Phytophthora cinnamomi* as compared with roots maintained continuously under oxygen concentrations of 7 mg/L. Symptom development in lateral roots progressed more rapidly in roots that had been stressed with low oxygen than in roots maintained under high oxygen. Maintenance of pine seedlings at oxygen concentrations of 0.25–1.0 mg/L for 12 and 24 hr before inoculation had no subsequent effect on root susceptibility to infection or the rate of symptom development in infected roots of either pine species. Results suggest that essentially anaerobic conditions are necessary in the rhizosphere before pine root tips are predisposed to attack by *P. cinnamomi*. Further, no evidence was found to support the hypothesis that differences in tolerance to low soil oxygen concentrations between loblolly and shortleaf pine are linked to their relative susceptibilities to infection by *P. cinnamomi*.

Plant species are known to vary in their tolerance to soil saturation and the low oxygen environment that results under this condition (16,17,27). Although definitive comparative studies have not been conducted on the tolerance of loblolly pine (*Pinus taeda* L.) and shortleaf (*Pinus echinata* Mill.) pine to low soil oxygen concentrations, several authorities have considered loblolly to be the more tolerant of the two species (15,16,28). Loblolly pine is rated as a moderately flood tolerant species, whereas shortleaf pine is considered to be among the least tolerant of the forest tree species (16). Where the range of these two species overlap, their ecological niches tend to be complimentary, with loblolly pine favored by the heavier-textured, wetter soils, and shortleaf pine by those sites that are lighter and drier (15,23). Low oxygen regimes affect both pine species, although Zak (28) concluded that loblolly pine exhibited greater tolerance to poor soil aeration than did shortleaf pine.

Soil types upon which littleleaf disease of pine has been most severe typically have poor internal drainage (3,4) and can have water tables that are perched for extended periods during the winter and spring months, particularly in years of high rainfall (13,14). In addition, the subsoil consistence of high hazard sites tends to be firm and plastic, and mottling typical of low aeration is present in some soils (3,14). The importance of poor internal drainage in the development of littleleaf disease has been assumed to be related to the production and dissemination of zoospores by *Phytophthora cinnamomi* Rands (2,28).

Soil oxygen concentration is regulated by all factors that affect diffusion coefficients, and by all factors that affect soil respiratory activity. Primary factors affecting the diffusion coefficient of oxygen into soil are soil moisture content and soil structure (11). Oxygen has a slow diffusion rate into, and a low solubility in, saturated soils and, therefore, oxygen may be depleted in sites of high metabolic activity (8,9,12,25). Oxygen levels in soil can decrease from 21 to 0% by volume in less than 24 hr if oxygen consumption is high (21). In addition, due to the heterogeneous nature of soil, some anoxic microsites may occur in soil even though the average oxygen concentration may be close to atmospheric levels (11).

The varying degrees of oxygen deficiency experienced by roots in saturated soils can cause physiologic damage resulting from both the direct and indirect effects of low oxygen concentrations, and this damage may predispose roots to infection (8,9,19,25). Kuan and Erwin (20) found that mortality of alfalfa (*Medicago sativa*) seedlings due to root rot caused by *P. megasperma* increased as the number of days of preinoculation soil saturation increased. Likewise, cultivars of *Rhododendron* spp., which were otherwise resistant to Phytophthora root rot, developed severe disease symptoms when root systems were flooded for periods of 48 hr before inoculation with *P. cinnamomi* (1).

Low oxygen conditions in the rhizosphere, which have been induced with nitrogen gas before inoculation, have predisposed roots to infection by fungi. Bean (*Phaseolus vulgaris*) plants exposed to low soil oxygen conditions for a period of 3 days were predisposed to attack by *Fusarium solani* f. sp. *pisi*, which otherwise is nonpathogenic on bean (22). In studies of root and crown rot of Mahaleb cherry (*Prunus mahaleb*) seedlings caused by *P. cryptogea*, reduction of soil atmosphere to 0.5% oxygen for a 24-hr period after inoculation greatly increased disease severity as compared with seedlings maintained in soil atmospheres of 2.5 and 21% oxygen (26).

The purpose of our study was to determine if exposure of loblolly and shortleaf pine roots to low oxygen concentrations for varied time periods before inoculation could alter root susceptibility to infection by *P. cinnamomi* and, if applicable, to determine if responses to low oxygen differed for the two pine species.

MATERIALS AND METHODS

Seedling and zoospore production. Loblolly and shortleaf pine seedlings were grown from seed in sand culture as previously described (10). Seed were obtained from the International Forest Seed Co., Birmingham, AL. Plants were grown in growth chambers at 24 ± 1 C with a 16-hr photoperiod for 6–7 wk. Light intensity in growth chambers was approximately 1,750 ± 50 lx.

Zoospore inoculum was produced as described previously (10), and quantified and handled as follows. Upon release of zoospores from sporangia, spores were poured through four layers of sterile cheesecloth, mixed gently, and five 10-ml samples were immediately withdrawn and placed in test tubes. Zoospores in stock solutions were held at 18 C until used for inoculations. Test tubes containing zoospores were placed on a vortex mixer for 30 sec, and 10 counts of cysts were made for each sample with the aid of a hemacytometer. Mean zoospore concentration of each sample was determined, and an overall mean concentration

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for the stock solution was calculated. Zoospore stock solutions were shaken for approximately 1 min to encyst and thoroughly mix spores. Appropriate dilutions then were made.

Application of low oxygen treatments. Plants to be inoculated were removed from sand culture by immersing pots in water and permitting sand to wash out of pots and away from root systems. Intact plants were removed from pots without exerting force, and seedlings were placed in holding chambers containing modified Ladiges nutrient solution (10). Holding chambers were Plexiglas, with walls 7 mm thick, a height of 15 cm, and a diameter of 20 cm. Chambers had a 1-cm diameter hole in the side wall through which ambient air and nitrogen was pumped into the nutrient solution. Tops of chambers had 12 2.2-cm-diameter holes through which seedlings were placed. Styrofoam plugs, 3 cm in diameter and slit lengthwise to the middle, served as supports for seedlings. Chambers were wrapped with aluminum foil to maintain roots in constant darkness. Each chamber contained a stir bar and was placed on top of a stirrer set at slow speed to maintain a constant circulation of nutrient solution across root surfaces. Light and temperature conditions within growth chambers were as described above.

Six to eight holding chambers were used, depending on the number of treatments in a particular experiment. Holding chambers designated for high oxygen levels (6.6–7.4 mg/L) received ambient air continuously. Purified nitrogen was bubbled into nutrient solutions of holding chambers designated for the low oxygen treatments. Delivery rate of nitrogen into tanks was regulated with a flow meter, and rates varied from approximately 250 cc/min for the 0.5–1.0 mg/L oxygen range to 1,150 cc/min for the dissolved oxygen concentration below 0.25 mg/L. Desired oxygen levels were attained in holding tanks before initiation of the experiment. Difficulties were encountered in maintaining tanks at specific oxygen concentrations and in maintaining tanks in each treatment at equal concentrations. Therefore, oxygen ranges had to be used for comparative purposes.

Four separate experiments were conducted. The low oxygen concentration in solution was maintained below 0.25 mg/L in the first and second experiments; in the range of 0.25–0.50 mg/L in the third experiment; and in the range of 0.50–1.0 mg/L in the fourth experiment. Control tanks that were maintained at high oxygen levels (6.6–7.4 mg/L) received ambient air continuously. Three replicates (blocks) were conducted over time for each experiment. In the first, third, and fourth experiments, seedlings of each species were transferred from high to low oxygen concentrations at 24 and 12 hr before inoculation. In the second experiment, seedlings were transferred from the high to low oxygen concentrations at 24, 12, and 6 hr before inoculation. In all experiments, control seedlings (i.e., 0 hr low oxygen) were maintained in holding chambers with nutrient solution at high oxygen concentrations for 24 hr before inoculation.

Oxygen concentrations in solution were determined with a YSI Model 58 Dissolved Oxygen Meter and YSI 5720A BOD Bottle Probe (Yellow Springs Instrument Co., Inc., Yellow Springs, OH). At the initiation of each replicate of an experiment and each time seedling transfers were made, oxygen concentrations in solution were determined and recorded. Temperatures of nutrient solutions also were recorded. Nutrient solution pH was determined at the end of the treatment periods.

Inoculation, incubation, and infection assessment. At the end of the low oxygen treatment period, seedlings were removed from holding tanks and inoculated. Low and high inoculum concentrations were used in all experiments, approximately 14 (14.4 ± 0.13) and 56 (56.6 ± 0.89) spores/ml, respectively. These concentrations were selected based on the results of previous studies (10) and preliminary low oxygen experiments. Four seedlings were used for each species, treatment, and zoospore concentration combination. All seedlings were exposed to zoospore cysts in 1,000-ml beakers for 3-hr periods at 24 C and subsequently incubated in holding tanks for 48 hr under high oxygen conditions. Root tips then were severed, surface-disinfested, plated on PCH agar medium (24), and assessed for the presence of *P. cinnamomi* as previously described (10). Roots of the four seedlings for each species, treatment, and inoculum concentration were pooled within each replicate. For each replicate, two seedlings of each species were used as nonstressed, uninoculated controls, and two seedlings of each species were used as uninoculated controls maintained for 24 hr in the low oxygen treatment. Observations were made on controls throughout experiments, and roots were subsequently assessed for *P. cinnamomi*.

Statistical designs and analyses. The statistical design for the assessment of the effect of dissolved oxygen concentration on root susceptibility was a split-split plot within a randomized complete block design. Each experiment was analyzed separately. Each replicate within an experiment was considered a block, low oxygen durations were whole plots, spore concentrations were subplots, and pine species were sub-subplots. Percentage infection of root tips was determined from the number of infected roots among all roots pooled for the four seedlings in each species, inoculum concentration, and low oxygen duration combination of each replicate. The proportion of roots infected was transformed by the logit transformation (5) for the analysis of variance.

RESULTS

Results of experiments one and two were similar and, therefore, of the two experiments, only the results of the latter are presented. Exposure of shortleaf and loblolly pine roots to oxygen levels below 0.25 mg/L for durations of 6–24 hr before inoculation with *P. cinnamomi* increased root susceptibility in both species (Fig 1; $P < 0.05$). Similar responses were obtained for both species at 14 and 56 spores/ml, although the percentage of roots infected was greater at the higher spore concentration ($P < 0.001$). Among spore concentrations and low oxygen durations, shortleaf pine roots were infected with greater frequency than loblolly pine roots ($P < 0.01$). The low oxygen duration $\times$ pine species interaction was nonsignificant ($P > 0.05$) for this experiment.

Considerable variation was observed among replicates within experiment two. At 14 spores/ml, variation among replicates for percent infection of nonstressed lateral roots was relatively small for both species (range 2.7–22.5%), whereas at 56 spores/ml, the range was considerably larger for loblolly (10.2–54.8%) and shortleaf pine (5.5–69%). The magnitude of the variation among replicates was similar for roots exposed to the low oxygen regimes for varied durations.

In experiment three, exposure of shortleaf and loblolly pine roots to low oxygen regimes in the 0.25–0.50 mg/L range before inoculation had no subsequent effect on root susceptibility to infection by *P. cinnamomi* (Fig. 2; $P > 0.05$). Among inoculum concentration and low oxygen durations, shortleaf pine roots again were infected with greater frequency than loblolly pine roots ($P < 0.05$) in this experiment. Low oxygen levels in the 0.5–1.0 mg/L range before inoculation also had no subsequent effect on the susceptibility of shortleaf and loblolly pine roots (Fig. 3; $P > 0.05$).

New foliage and shoots of pine seedlings of both species typically wilted within 3–6 hr after being exposed to the lowest oxygen concentrations (< 0.25 mg/L). The wilting was of short duration, and within 9–12 hr, seedlings had regained turgor despite the continuation of the low oxygen condition around the root. Lateral root tips of seedlings exposed to this oxygen concentration often developed a bluish to purplish discoloration within the 24-hr stress period. Wilting was not exhibited in seedlings held at an oxygen concentration of 0.25–1.00 mg/L, and no discoloration occurred.

Roots of uninoculated seedlings normally survived when stressed for 24 hr with oxygen concentrations of less than 0.25 mg/L. In one experiment, very fine roots of oxygen-stressed control plants for each species became brown and died during the 48-hr incubation period. Otherwise, lateral root tips of uninoculated, stressed seedlings appeared healthy, although they often were stunted.

Symptom development was rapid in roots of inoculated seedlings that had been stressed with oxygen concentrations of less than 0.25 mg/L. At 14 spores/ml, some roots of seedlings

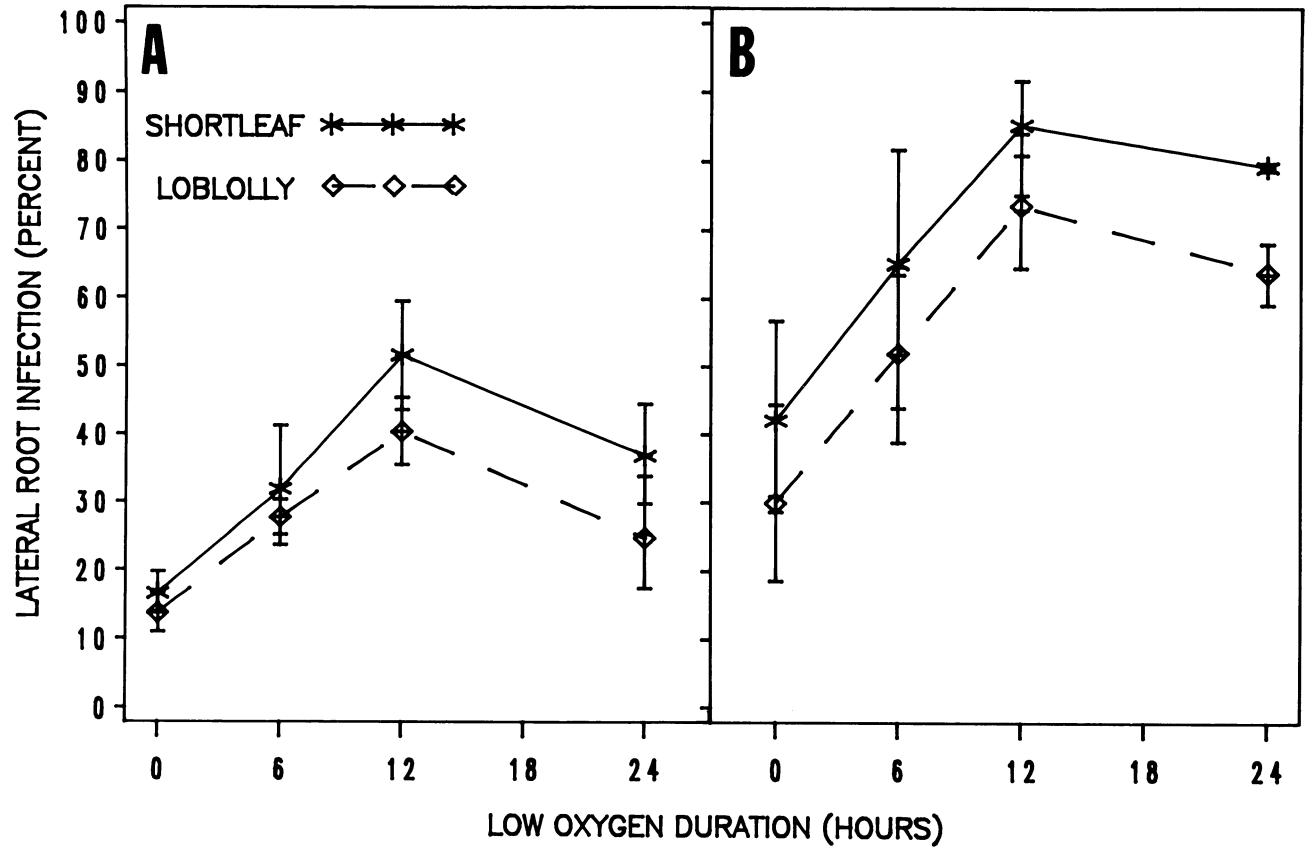

Fig. 1. Influence of preinoculation low oxygen (< 0.25 mg/L) duration on the subsequent infection of shortleaf and loblolly pine lateral roots inoculated with zoospore cysts of *Phytophthora cinnamomi* at concentrations of **A,** 14 and, **B,** 56 spores/ml.

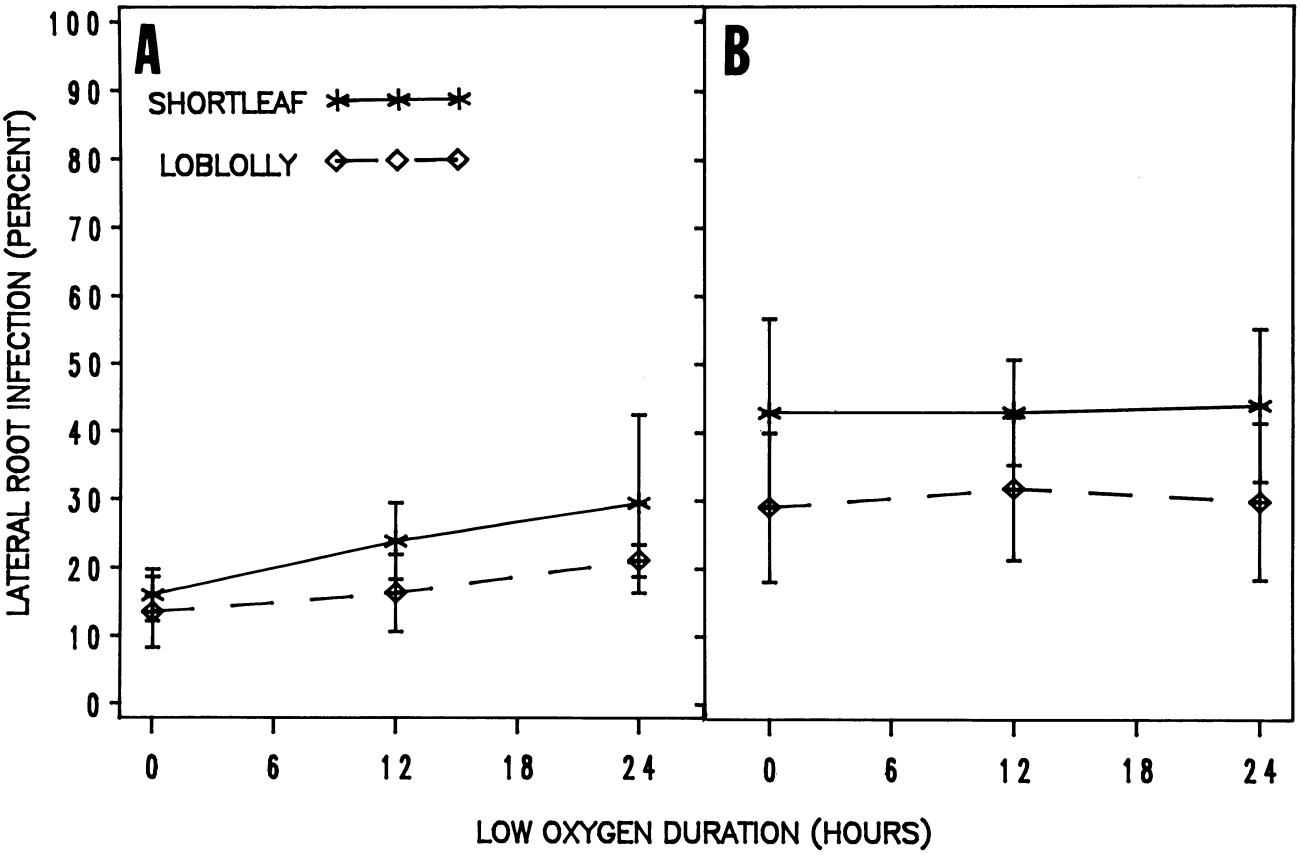

Fig. 2. Influence of preinoculation low oxygen (0.25–0.50 mg/L) duration on the subsequent infection of shortleaf and loblolly pine lateral roots inoculated with zoospore cysts of *Phytophthora cinnamomi* at concentrations of **A,** 14 and, **B,** 56 spores/ml.

stressed for 12 and 24 hr were grayish-brown to light-brown at the end of the 48-hr incubation period, whereas nonstressed roots appeared symptomless, despite the presence of some infections (Fig. 1). At 56 spores/ml, many lateral root tips of stressed seedlings had a dark brown discoloration whereas most roots of nonstressed seedlings remained white and succulent, although some evidence of infection was observed in some roots.

Temperatures within tanks normally ranged from 23 to 26 C. Measurements made at the end of the low oxygen treatment period indicated that nutrient solution essentially remained unchanged from the initial pH 5.2 when oxygen concentrations were maintained below 0.25 mg/L. At the high oxygen concentrations, nutrient solution pH dropped to an average of 4.3. The pH levels dropped to approximately 4.3 in both low and high oxygen environments in experiments in which low oxygen concentrations were maintained in the 0.5–1.0 mg/L range. No pH measurements were taken for experiments in which oxygen concentrations were maintained in the 0.25–0.50 mg/L range.

DISCUSSION

Our results presented here agree with those of other studies (1,20,22,26) and indicate that stress induced by low oxygen can predispose roots to disease caused by some soilborne pathogens. We also have shown that essentially anaerobic conditions are necessary in the root zone before roots of loblolly and shortleaf pine are predisposed to infection.

There are several theories regarding the enhanced infection or disease severity after periods of low oxygen stress. Kuan and Erwin (20) believed that the higher mortality of alfalfa seedlings in their study was related partly to an increase in the quality and quantity of exudates from roots following periods of soil saturation, which, in turn, exerted a secondary chemotactic effect on zoospores and rendered plants more susceptible to disease. In the present study, experiments were conducted with zoospore cysts and, therefore, enhanced susceptibility of seedlings stressed with oxygen concentrations below 0.25 mg/L cannot be attributed to attraction of zoospores to root surfaces. However, germ tubes of cysts have been observed to exhibit orientation toward roots (29), and possible increases in quantity and quality of exudates after exposure to low oxygen concentrations may have had an enhancing effect on germ tube stimulation and orientation toward pine root surfaces in our studies. Another possibility is that the number of suitable sites for successful penetration and establishment of *P. cinnamomi* in roots may have increased after the periods of oxygen stress and, therefore, the probability of root infection also increased. Likewise, as the inoculum concentration was increased from 14 to 56 spores/ml, the probability was greater of a germ tube contacting a suitable, infectible site.

Blaker and MacDonald (1) proposed that, because oxygen deficiency can disrupt many metabolic pathways in plants, oxygen deficiency could function in predisposition by impairing the ability of a plant to resist pathogen invasion. This hypothesis also was supported by Wilcox and Mircetich (26), who found that relative to seedlings maintained at high oxygen concentrations, a short-term exposure to a low oxygen environment during post-inoculation periods significantly increased disease severity in Mahaleb cherry seedlings infected by *P. cryptogea*. In our study, symptom development appeared to proceed more rapidly in oxygen stressed roots as compared with roots maintained continuously under high oxygen concentrations. We used non-motile spores and relatively low spore concentrations; and therefore, we do not believe that the rapid symptom development in stressed roots was due exclusively to an increase in the total number of infections on a single root. Rather, we believe that the rapid symptom development in stressed roots may have been due primarily to impaired plant resistance mechanisms and subsequent rapid colonization of host tissues by *P. cinnamomi*.

Seedling wilting and subsequent restoration of turgor in experiments conducted at oxygen concentrations below 0.25 mg/L was a direct result of the low oxygen environment. When considering the effect of low oxygen on roots, a distinction should

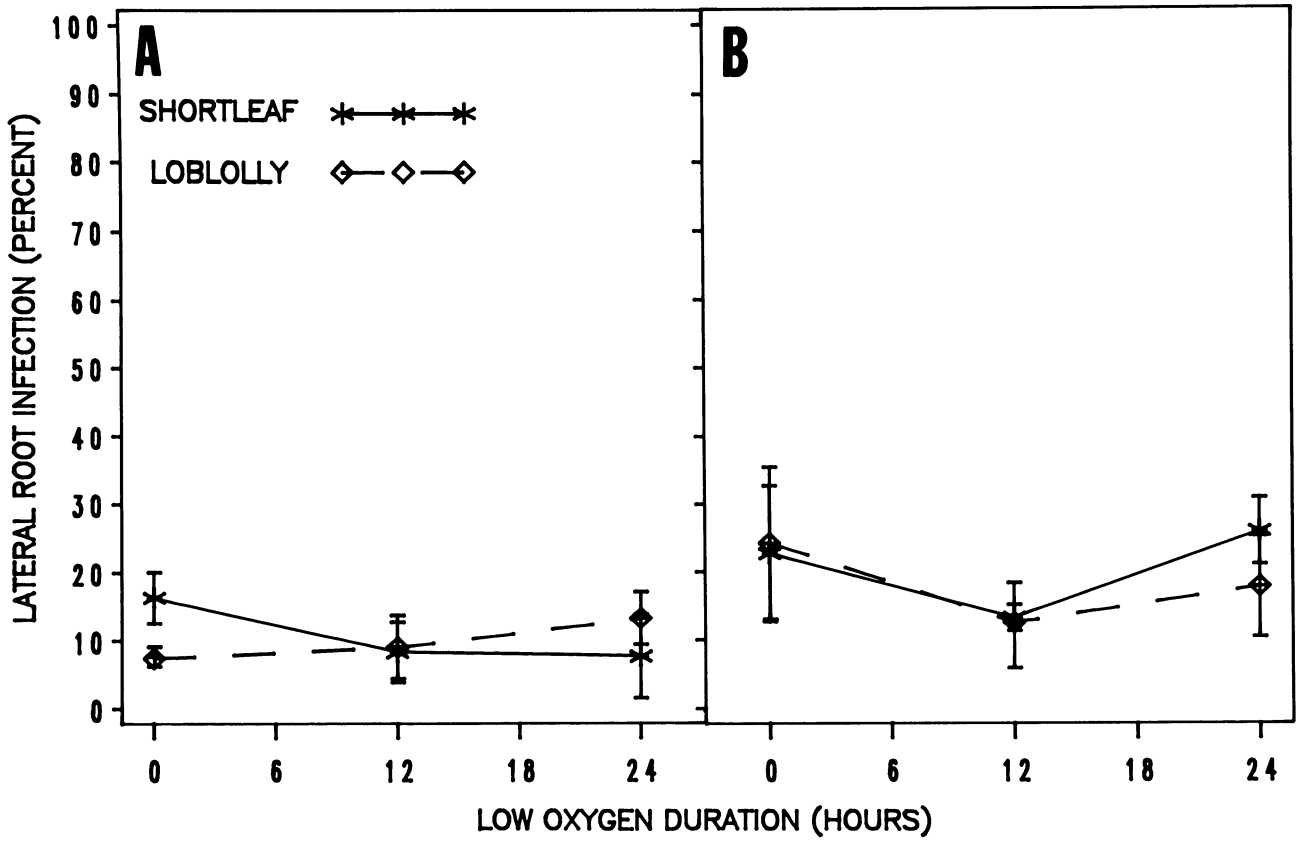

Fig. 3. Influence of preinoculation low oxygen (0.5–1.0 mg/L) duration on the subsequent infection of shortleaf and loblolly pine lateral roots inoculated with zoospore cysts of *Phytophthora cinnamomi* at concentrations of **A,** 14 and, **B,** 56 spores/ml.

be made between plants that have developed originally under conditions of little or no oxygen and those that are grown under aerobic conditions (7). A sudden cessation of aeration, or an event of sudden flooding, exerts a harmful effect on a plant for which the root system has developed during a period of ample oxygen supply (7). The first effect of flooding or deficient aeration on plants is an increase in viscosity of cell protoplasm and a concomitant decrease in root permeability, thus, limiting water uptake (18,19). Wilting is likely to be the first symptom of oxygen deficiency in the rhizosphere if atmospheric conditions are satisfactory for transpiration (18). Eventual damage to root cells causes an increase in permeability and a temporary alleviation of wilt symptoms (19). Periods of temporary wilting have been observed in studies with avocado during the first day of exposure to low oxygen concentrations of 0.05–0.5% (6). As we noted in pine, a purplish discoloration also was associated with the avocado root tips exposed to low oxygen.

Blaker and MacDonald (1) observed that plants in which disease development was most rapid and disease severity greatest had exhibited wilting when plants were flooded during a 48-hr period before inoculation. They attributed wilting to high transpirational demand and severe oxygen deficiency that they believed arose in the rhizosphere during flooding. In our growth chamber study, wilting was observed only under extremely low oxygen concentrations (<0.25 mg/L), and only those seedlings subsequently exhibited an increase in susceptibility to infection by *P. cinnamomi*. Further investigations are necessary to determine if there is an interactive effect of transpirational demand and low oxygen concentrations in the rhizosphere for host predisposition to infection.

The results of our study do not support the hypothesis that the relative tolerance of loblolly pine to low oxygen conditions is linked to its lower susceptibility to infection by *P. cinnamomi*, as compared with shortleaf pine. The degree of increase in lateral root infection was similar in both species following exposure to all low oxygen concentrations. However, the low oxygen regimes were administered over a very short duration (6–24 hr). Also, at the initiation of low oxygen treatment periods, there was an immediate change in oxygen status of roots. Possibly, more attention should be given to the effect of chronic low oxygen concentrations in the range of 0.25–1.0 mg/L, or adjusting roots slowly to the low oxygen concentrations to which seedlings are to be subjected. Because no host predisposition was exhibited when oxygen concentrations were maintained in the 0.25–1.0 mg/L range, we suggest that essentially anaerobic conditions are necessary to alter root susceptibility.

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