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Influence of Soil Aluminum and pH on Armillaria Root Rot in Douglas-fir in Western Washington

Abstract

It was hypothesized that high extractable Al concentrations in acid soils in young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations in western Washington would induce root stress and increase susceptibility to Armillaria root disease. In contrast, however, soils from 5 to 35 year-old Douglas-fir stands with a high severity of Armillaria root disease (13-25 infected trees/ha) had significantly lower ($p < 0.05$) average water extractable Al concentrations (9.0 ± 3.1 μg Al/g) than soils with low disease severity (0-12 infected trees/ha) (22.4 ± 5.3 μg Al/g). Soil pH and 2N KCl extractable Al averaged 4.46 ± 0.10 and 313 ± 164 μg Al/g, respectively, in low severity sites and 4.73 ± 0.20 and 149 ± 69 μg Al/g, respectively, in high severity sites, but were not significantly different between low and high severity sites. To examine the specific effects of Al and pH, growth responses of isolates of *Armillaria ostoyae* (Romagn.) Herink from Douglas-fir plantations were examined in pure culture. Diameter growth on soil extract agar declined as water extractable Al increased. In addition, diameter growth decreased with increasing Al in non-buffered media. The separate effects of Al and pH, however, could not be determined with this experiment; Al levels ranged from 0-200 mg/L, but pH declined from 5.8 to 2.6. Diameter growth decreased rapidly with increasing Al levels in buffered media at pH 4, but less rapidly at pH 5 or 6. Without Al in the media *Armillaria* growth increased with decreasing pH. Both Al and pH influenced *Armillaria* growth in culture and had interacting effects.

Introduction

In the Pacific Northwest, *Armillaria* spp. causes the most common and widely distributed root disease of western conifers (Hadfield *et al.* 1986). Recent studies have shown *Armillaria* to consist of a complex of at least nine biological species in North America (Anderson 1986) with the pathogenic species on most conifers in the west thought to be *A. ostoyae* (Romagn.) Herink (Morrison *et al.* 1985, Wargo and Shaw 1985).

Although the factors that control pathogenicity of *Armillaria* have been widely studied, they are not well understood (Wargo and Shaw 1985). Because this fungus commonly attacks stressed trees, factors affecting both the vitality of the tree and the vitality of the fungus must be considered. General factors such as environmental stress (Wargo 1980) and habitat type (McDonald *et al.* 1987a, 1987b) have been related to the incidence of Armillaria root disease. Specific soil factors, such as nutrition and pH, may also be important (Wargo and Harrington 1991). Redfern (1978), Shields and Hobbs (1979), and Singh (1983) found that low soil pH favored disease development under field conditions, but this relationship was not clear in all studies (Redfern and Filip 1991).

High aluminum concentrations in acid soils cause plant stress and there has been much interest in determining relationships between soil pH and Al toxicity to roots (Ulrich 1983). In the soil solution, Al occurs in a variety of ionic forms, such as Al^{3+}, $Al(OH)^{2+}$ or $Al(OH)_2^{+}$ (Parker *et al.* 1988). The most toxic form is assumed to be Al^{3+}, but it is generally in low concentrations in soil solutions because of low solubility. As soil pH is lowered Al becomes more soluble. Aluminum toxicity generally does not occur in soils with a pH above 5.5, but it becomes increasingly severe as the pH drops below 5 (Ulrich 1983).

In 1985 the authors noted that Armillaria root disease was killing young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees near Hoquiam, Washington in areas with relatively acid soil (<pH 5). It was hypothesized that high soil Al concentrations were causing root stress, thus making trees more susceptible to Armillaria root disease. There have been relatively few studies on the effects of Al on soil microbes and plant pathogens. However, it has been shown that soil Al can act as a fungitoxin (Ko and Hora 1972), and it can reduce soil pathogen levels (Hartley 1928, Orellana *et al.* 1975, Muchovej *et al.* 1980) as well as the growth of mycorrhizal fungi (Thompson and Medve 1984, Entry *et al.* 1987). It is not clear how soil pH and Al influence host/*Armillaria* relationships.

This study was initiated to determine: (1) relationships between soil extractable Al and pH and the incidence of Armillaria root rot in Douglas-fir plantations in western Washington, (2) the effect

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TABLE 1. Location of study sites in western Washington, Armillaria root disease severity, stand age, elevation, soil pH and extractable Al.

Site No.	Armillaria severity[1]	Location from nearest town (distance in km-bearing)	Stand age (years)	Elevation (m)	pH	2N KCl extractable Al (μg/g)	Water extractable Al (μg/g)
1	High	Hoquiam (19-NW)	5	30	4.90	312	8.3
2	High	Hoquiam (18-NW)	20	30	4.85	321	3.4
3	High	Blyn (14-SW)	20	910	4.62	15	0.5
4	High	Blyn (10-SW)	25	660	4.46	4	1.1
5	High	Silver Creek (7-S)	15	250	4.26	5	7.5
6	High	Silver Creek (10-SW)	20	200	4.19	3	5.0
7	High	Silver Creek (9-S)	25	250	4.47	1	6.7
8	High	Lebam (6-SW)	35	210	5.02	577	20.1
9	High	North Bend (3-NW)	10	180	5.84	109	28.6
Average[2] ± SE for pH and extractable Al.			20	302	4.73 ± 0.20^a	149 ± 69^a	9.0 ± 3.1^a
10	Low[3]	Hoquiam (8-NE)	5	60	4.88	1075	37.8
11	Low[3]	Hoquiam (10-NE)	20	90	4.30	1958	50.4
12	Low	Blyn (5-S)	15	270	4.77	6	1.6
13	Low	Blyn (6-S)	18	670	4.98	7	2.1
14	Low	Blyn (7-S)	22	550	3.77	27	0.9
15	Low	Silver Creek (8-SW)	10	150	4.20	1	10.3
16	Low	Silver Creek (15-SW)	15	100	3.81	36	18.4
17	Low	Silver Creek (12-S)	20	200	4.12	9	22.4
18	Low	Silver Creek (6-S)	20	300	4.29	19	23.1
19	Low	Silver Creek (5-S)	25	200	4.51	20	9.3
20	Low	Raymond (6-E)	10	60	4.54	4	31.8
21	Low	South Bend (9-W)	10	60	4.97	271	21.3
22	Low[3]	South Bend (9-W)	10	50	4.87	632	62.6
Average ± SE for pH and extractable Al.			15	212	4.46 ± 0.10^a	313 ± 164^a	22.4 ± 5.3^b

[1] High severity (13-15 infected trees/ha); low severity (0-12 infected trees/ha).

[2] Averages followed by a different letter in the same column are significantly different ($p < 0.05$).

[3] No Armillaria root rot in these stands.

of soil extracts on growth of *Armillaria* in culture, and (3) the influence of Al and pH on *Armillaria* growth in culture.

Materials and Methods

Study Sites

Twenty-two Douglas-fir stands in western Washington were selected (Table 1). Sites 1-9 had high *Armillaria* severity (13-25 diseased trees/ha) while sites 10-22 had low disease incidence (0-12 diseased trees/ha). All stands were plantations except site 8. Stand ages varied from 5 to 35 years, averaging 20 years in high severity sites and 15 years in low severity sites (Table 1). Young stands were selected since *Armillaria* is less of a problem in older Douglas-fir stands (Hadfield *et al.* 1986). The stands were located in the coast range except site 9 which was located in the foothills of the Cascade Mountains. Elevations ranged from 30 to 910 m with similar average elevations in high (302 m) and low (212 m) severity sites (Table 1).

Soil Chemistry

Soil samples were taken from three random locations at each of the 22 sites. At each location five systematic samples were taken from the top 5 cm of mineral soil, bulked and transported to the laboratory for analysis of extractable Al and pH. The top 5 cm was sampled because many of the roots and microbial activity are found in this zone. Rhizomorphs also commonly occur near the soil surface. Water extractable and 2N KCl extractable Al were determined using a modification of procedures by Barnhisel and Bertsch (1982). Two g of field soil were shaken in 200 ml of deionized water or 20 ml of 2N KCl for 4 hours and centrifuged. Solutions were analyzed on an IL 951

Atomic Absorption Spectrophotometer. Results were expressed as μg Al/g oven dry soil (105°C). Soil pH was determined using a 1:1 (volume) soil distilled water mix and a pH meter (Fisher Accumet Model 210).

Source of *Armillaria* Isolates

Three diploid isolates of *Armillaria* were obtained from mycelium fans growing in infected but still living Douglas-fir trees in western Washington. Two isolates came from coastal sites near Hoquiam, while the third isolate was from a low elevation site in the Puget Sound area near Snohomish. All three diploid isolates were identified as *Armillaria ostoyae* by cross plating using the method described in Guillaumin *et al.* (1991) with known testers provided by Dr. Duncan Morrison, Pacific Forestry Research Center, Victoria, British Columbia.

Armillaria Growth in Culture on Soil Extract Medium

The three *Armillaria* isolates were grown on unamended soil extract agar from Douglas-fir stands at Hoquiam (sites 1 and 11), Lebam (site 8), Raymond (site 20), and a fifth site near Snohomish, Washington, using technique M-26 outlined in Stevens (1974). Five replicate plates were used for each isolate and diameter growth was measured after 60 days of incubation at 20°C. Sixty days was used because of the very slow growth on the low nutrient soil extract medium. Some of the cultures developed rhizomorphs, but they were not included with the diameter measurements. Rhizomorph development tended to increase with decreasing pH. Fungal biomass is a better measure of growth than diameter because it includes rhizomorphs. Biomass was determined in a series of tests (Browning 1987). The linear correlation between biomass and diameter growth was positive ($r = 0.41$, $n = 90$) and significant ($p < 0.01$). Shaw (1985) also found that diameter and *Armillaria* dry weight were related in younger colonies. Thus it was felt that diameter growth correctly reflected growth trends even though rhizomorphs were not measured. Rhizomorphs are important in disease spread in the field.

Determination of Growth in Culture in Non-Buffered and Buffered Media

Non-Buffered Media. Isolates were grown in petri plates on 2% malt agar containing different amounts of Al. $AlCl_3 \cdot 6H_2O$ salt was used as the source of Al^{3+} at concentrations of 0, 10, 25, 50, 100, and 200 mg Al/L. These concentrations were selected since they overlap the range of water extractable Al concentrations from the soil (0.5-62.6 μg/g) and fall in the range of 2N KCl extractable Al (1-1958 μg/g) (Table 1). The units μg Al/g in soil and mg Al/L in solution are similar but not exactly equivalent because soil bulk density was not 1.0. Bulk densities typically ranged from 0.5 to 0.8 in these soils. Concentrations of Cl (0-788 mg/L) in the $AlCl_3 \cdot 6H_2O$ media are typical of those used in culture media (Stevens 1974, Robinson 1978) and should have had no influence on growth of *Armillaria.* The media were seeded with the three isolates on separate plates using a 5 mm cork borer and 5 replications of each treatment. Media pH was taken before autoclaving. Cultures were incubated at 20°C. Diameter growth of mycelium was measured in each plate after 30 days by averaging two perpendicular measurements.

Buffered Media. One percent malt extract media were buffered to pH 4, 5, and 6 by adding 0.1 M citric acid and 0.1 M trisodium citrate (McKenzie 1969). 1.0 N KOH and 1.0 N HCl were used to adjust the final pH. $AlCl_3 \cdot 6H_2O$ was added in concentrations of 0, 100, 200, and 300 mg Al/L. The media in petri plates were seeded with plugs of the three isolates using a 5 mm cork borer and 10 replications per treatment. Cultures were incubated at 20°C. Diameter growth of the mycelium was measured in each plate after 30 days by averaging two perpendicular measurements.

Statistical Analysis

Two-way analysis of variance was used to examine relationships among fungal growth, Al concentration and pH in buffered Al media at different pH levels. One-way analysis of variance was used to test growth differences among fungal isolates. A Newman-Keuls multiple-range test was used to determine significance. Regression analysis was used to examine relationships between soil pH and extractable Al concentrations, fungal growth and Al concentrations in soil extract media, and fungal growth and Al and pH in non-buffered and buffered media. Student t-tests were used to determine if means of soil pH, and water extractable and 2N KCl Al from high and low severity stands were different. The statistical package SYSTAT (Wilkinson 1989) was used on an Apple Macintosh IIci computer.

Results and Discussion

Relationships Between *Armillaria* Incidence and pH and Al in the Field

It has been difficult to find strong relationships between expression of Armillaria root disease and field variables because many factors are involved, such as host vigor, abiotic stresses (light, temperature, moisture, nutrients, pH), presence or absence of inoculum, insects, other diseases, and management activities such as partial cutting (Wargo and Harrington 1991). Reaves *et al.* (1990) also suggested that burning may inhibit *Armillaria* by stimulating antagonistic fungi. We do not know the history of burning on our sites, however.

Armillaria is considered a disease of weakened trees (Wargo and Harrington 1991). Stress reduces host vigor and compromises host defenses. Aluminum toxicity to roots increases plant stress (Ulrich 1983) so it was hypothesized that Douglas-fir growing in soils in western Washington with the highest extractable Al concentrations would have the highest Armillaria root rot disease severity. However, the opposite situation was found. Sites with high disease severity had a significantly lower average water extractable Al concentration in the soil (9.0 ± 3.1 μg Al/g) compared to sites with low severity (22.4 ± 5.3 μg Al/g) (Table 1). No disease was observed on the sites with the highest water and 2N KCl extractable Al (Table 1).

It was expected that soils with the highest extractable Al concentrations would also be the most acidic since Al concentrations increase with decreasing pH (Ulrich 1983). However, there was not a significant relationship using regression analysis between soil pH and extractable Al in soils from the twenty-two sites. Soil pH and 2N KCl extractable levels were not significantly different between high and low severity sites. 2N KCl extractable Al averaged 149 ± 69 μg/g in low severity sites and 313 ± 164 μg/g in high severity sites (Table 1). Soil pH averaged 4.73 ± 0.20 and 4.46 ± 0.10 in high and low severity sites, respectively (Table 1). Although Redfern (1978), Shields and Hobbs (1979) and Singh (1983) found that low pH favored higher disease development under field conditions, Redfern and Filip (1991) suggested that data relating disease severity and soil pH in the field are generally inconclusive.

Because the influence of soil Al and pH on *Armillaria* severity was not clear from the field data, a series of laboratory experiments were undertaken to determine the influence of Al and pH on *Armillaria* growth in culture. This involved determination of growth on soil extract media and non-buffered and buffered media containing various concentrations of Al at different pH levels.

Armillaria Growth on Soil Extract Media

Average diameter growth of the three *Armillaria* isolates in culture on five soil extract agars is shown in Figure 1 in relation to water extractable Al concentrations from these soils. There were no significant differences in growth among the three isolates so pooled data were used. *Armillaria* diameter growth tended to decrease with increasing soil water extractable Al concentrations (Figure 1). The logarithmic regression ($r = -0.86$, $n = 5$) is significant at $p < 0.05$, but the linear regression is not ($r = -0.74$). Growth data of this type are commonly not linear. Correlations between *Armillaria* diameter growth and 2N KCl extractable Al and pH were not significant. These data tentatively support the data in Table 1 which show that soils with higher average extractable Al have lower disease incidence, while pH was not significant.

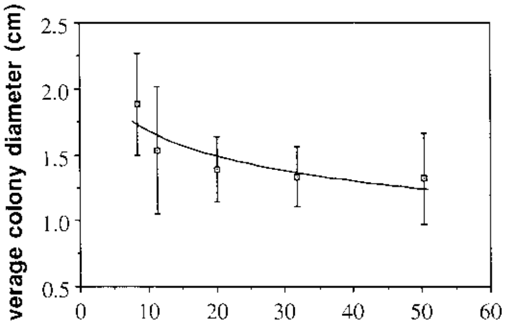

Figure 1. Average colony diameter after 60 days of three *Armillaria ostoyae* isolates from western Washington grown on soil extract agar in relation to water extractable Al from those soils. Standard errors and logarithmic regression line ($r = -0.86$, $n = 5$, $p < 0.05$)) are shown. The linear regression was not significant ($r = -0.74$, $n = 5$)

Armillaria Growth on Non-buffered and Buffered Media

In order to separate the effects of Al and pH on *Armillaria* growth in vitro, the three isolates were grown on both non-buffered and buffered media.

Again there were no significant differences in growth among the three isolates so pooled data were used. In the non-buffered Al media growth decreased with increasing Al (Figure 2). The correlation between fungal growth and media Al concentration was high ($r = -0.81$, $n = 90$, $p < 0.001$). These isolates of *Armillaria* appeared very sensitive to Al. Aluminum has been found by others to negatively influence the growth of fungi in culture (Firestone *et al.* 1983, Muchovej *et al.* 1980, Orellana *et al.* 1975, Thompson and Medve 1984). The independent effects of Al and pH, however, cannot be evaluated using an unbuffered medium since pH fell from 5.8 in the 0 mg Al/L treatment to 2.6 in the 200 mg Al/L treatment.

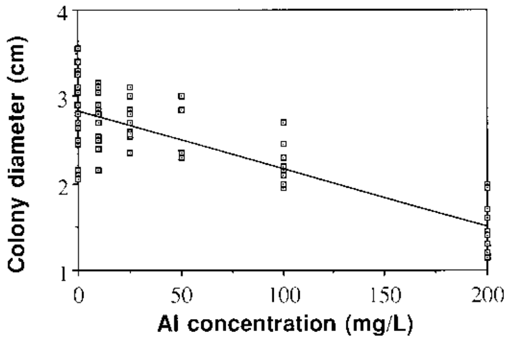

Figure 2. Colony diameter after 30 days of three *Armillaria ostoyae* isolates from western Washington in relation to Al concentration in non-buffered media. Media pH ranged from 2.8 (200 mg Al/L) to 6.0 (0 mg Al/L). $r = -0.81$, $n = 90$, $p < 0.001$ for linear regression line.

A buffered media was used to evaluate these independent effects. In buffered Al media at pH 4, growth of *A. ostoyae* decreased substantially with increasing Al (Figure 3A, $r = -0.84$, $n = 120$, $p < 0.005$). At pH 5 and 6 growth decline was less with increasing Al concentration (Figure 3B, $r = -0.41$, $n = 120$, $p < 0.01$ and Figure 3C, $r = -0.30$, $n = 119$, $p < 0.01$). Thus, growth seemed to be more affected by Al at pH 4 than at pH 5 or 6. A two-way ANOVA showed Al, pH, and the interaction between pH and Al to be significant. In nutrient solution studies of plants, it is well-documented that raising the pH generally relieves Al toxicity (Parker *et al.* 1988). It is unclear whether this is due to decreased solubility of Al^{3+} at higher pH, formation of non-toxic complexes, or a physiological response whereby low pH predisposes the plant to Al injury (Parker *et al.* 1988). What mechanism is involved with *Armillaria* is unknown.

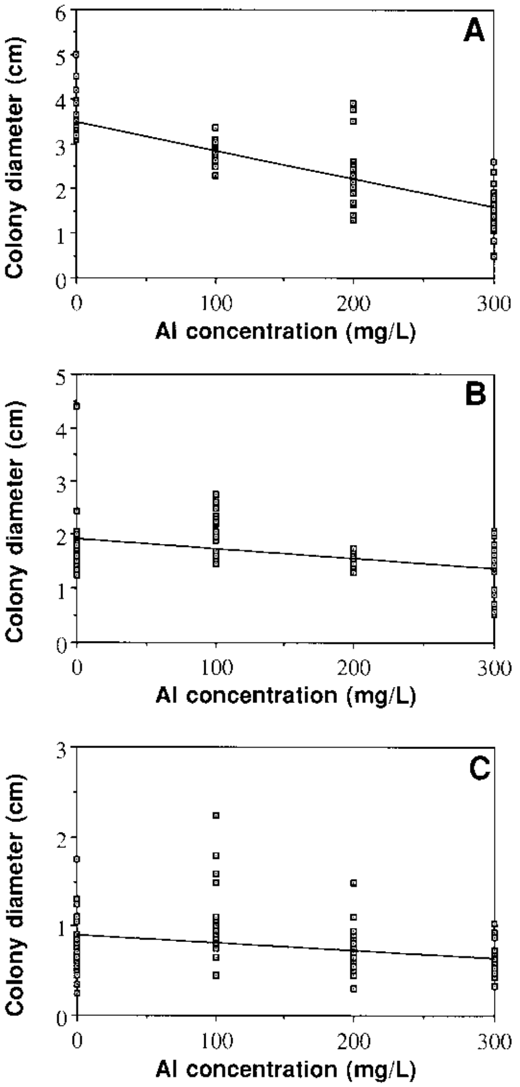

Figure 3. Colony diameter after 30 days of three *Armillaria ostoyae* isolates from western Washington in relation to Al concentration in buffered media at (A) pH 4, $r = -0.84$, $n = 120$, $p < 0.005$, (B) pH 5, $r = -0.41$, $n = 120$, $p < 0.01$ and (C) pH 6, $r = -0.30$, $n = 119$, $p < 0.01$.

Armillaria growth in culture was strongly influenced by media pH in the absence of Al. Colony diameter increased with decreasing pH (Figure 4) ($r = -0.92$, n 90, $p < 0.001$). The highest rate of growth was observed at pH 4. Morrison (1974) found that the effect of pH on *Armillaria* growth varied with the fungal isolate; some isolates grew best on acidic media while others grew best on alkaline media. Further work by Morrison reported by Redfern and Filip (1991) suggested that these differences were actually related to species. *Armillaria ostoyae* and *A. mellea* grew better in acidic soil whereas *A. gallica* was either unaffected by pH or favored by alkaline soil.

Douglas-fir Response to Al

Laboratory studies are helpful in examining responses of fungi to specific environmental factors, but they don't necessarily explain host response. Another factor to consider is host response to soil Al. Douglas-fir may not be as sensitive to Al as *Armillaria*. At pH 3.4 to 3.6, Douglas-fir seedling growth in solution culture was not negatively affected at concentrations as high as 4000 mg Al/L (Keltjens 1990), whereas *Armillaria* showed growth reductions at concentrations <300 mg Al/L at pH 4 (Figure 3A). Ryan *et al.* (1986a, 1986b) also found that Douglas-fir seedlings were relatively tolerant to high levels of Al. Furthermore, Keltjens (1990) suggested that in acidic forest soils with pH >4.0 and low Ca and Mg, moderate Al concentrations in the soil solution may play a beneficial role by alleviating the adverse effects of high H^+ concentrations in the soil solution. Organic acids in soil solutions can also ameliorate Al toxicity by complexing Al (Parker *et al.* 1988). The role of soil Al and pH in the Douglas-fir/Armillaria root rot relationship is not completely understood and needs further study.

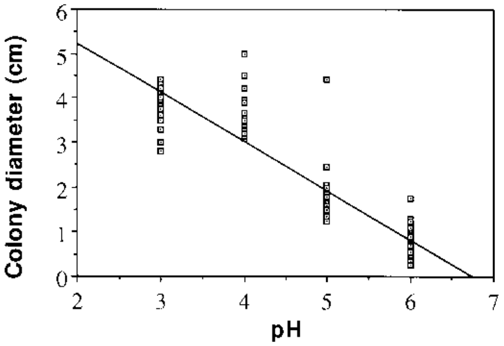

Figure 4. Colony diameter after 30 days of three *Armillaria ostoyae* isolates from western Washington in relation to pH in buffered media without Al. $r = -0.92$, $n = 90$, $p < 0.001$.

Acknowledgments

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