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Potassium fertilizer applied immediately after planting had no impact on Douglas-fir seedling mortality caused by laminated root rot on a forested site in Washington State

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Abstract

Phellinus weirii causes laminated root rot (LRR), a major disease affecting growth and survival of *Pseudotsuga menziesii* (Douglas-fir) and other commercially important conifer species throughout the Pacific Northwest. Increasing tree vigor and resistance to pathogens through application of K fertilizer is a suggested disease management strategy and one we wished to test. Plots were established with Douglas-fir seedlings planted densely (12,000 seedlings ha^{-1}) around stumps of LRR-killed trees on a harvested site west of the Cascade Range crest near Morton, Washington. Treatments, randomly assigned to plots, were: 224 kg K ha^{-1}, 448 kg K ha^{-1}, 224 kg K + 224 kg N ha^{-1}, and a no-fertilizer control, with 11 replicates. Roots of seedlings receiving the K + N treatment showed the only increase in phenol/sugar (P/S) ratios after one growing season, owing to a reduction in sugar concentrations. Although increases in P/S ratios are negatively correlated with fungal infection rates, the LRR mortality for all fertilizer treatments, including the K + N, was similar to the mortality on the no-fertilizer plots 7 years post-treatment. For this study site we concluded that the single application of K or K + N to Douglas-fir at the rates tested were not an effective management strategy for LRR.

Keywords: Defensive chemicals; Root disease; Plant nutrients; Laminated root rot

1. Introduction

Phellinus weirii (Murr.) Gilb., causes laminated root rot (LRR), a major disease affecting growth and survival of *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) and other commercially important conifer species. The disease is widespread throughout the range of Douglas-fir and is a frequent, and particularly disruptive, component of stands west of the crest of the Cascade Range in Washington and Oregon. When infected trees die or are cut, the fungus may continue to live saprophytically in colonized stumps. Infection in a replacement stand occurs when the roots from the new stand grow into contact with infected stumps or roots from the preceding stand. Additional details of the biology, distribution, and impact of LRR, relative susceptibility of host species, and options for management are summarized by Thies and Sturrock (1995) and Hansen and Goheen (2000).

The influence of tree nutrition in forest health, and fertilization as a tool to manipulate the nutritional status and vigor of conifers, has been the focus of numerous studies over the last 25 years, particularly in dry western inland forests. In 1980 the Intermountain Forest Tree Nutrition Cooperative (IFTNC) was organized at the University of Idaho, with initial efforts concentrated on studying the effect of N fertilization on growth and survival of Douglas-fir. It was observed that N fertilization often increased the growth of Douglas-fir, but the response seemed to be influenced by levels of potassium in soils (Mika and Moore, 1990). It was further noted that applying N at high rates where K levels were low sometimes corresponded with an increase in mortality for Douglas-fir and ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. (Mika and Moore, 1990; Mika et al., 1992; Moore et al., 1994).

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Waring (1987) highlighted the relationship between tree vigor and forest health by proposing that any type of stress (i.e. shading, drought, nutrient deficiencies and imbalances, or their combinations) causing physiological imbalances that lead to substantial reduction in vigor will reduce a tree's resistance to attack by pathogens and insects. This hypothesis was supported by results from various studies (Matson and Waring, 1984; Entry et al., 1986, 1991a, 1992; Waring et al., 1987). Entry et al.'s combined works (1991a,b, 1992) provided convincing evidence that changes in environmental parameters cause changes in root chemicals that influence fungal infection rates. The phenolics and lignin function as defensive compounds limiting fungal growth, whereas carbohydrates in various forms (sugars, starch, cellulose) supply energy used by fungi to degrade, deactivate, or outgrow the antifungal defenses. These antagonistic interactions have been demonstrated in culture for *Armillaria mellea* (Vahl.ex Fr.) Karst (Garraway et al., 1991) and for *Armillaria ostoye* with phenolic extracts from Douglas-fir bark (Entry et al., 1991b). The infection rates of conifer roots by *A. ostoye* decline with increasing ratios of phenolic/sugar (P/S) or lignin/sugar (L/S) concentrations (Entry et al., 1991a,b, 1992). The infection rate of Douglas-fir seedlings by *P. weirii* is also negatively correlated with increasing phenol/cellulose or lignin/cellulose ratios (Entry et al., 1994).

Results of this kind suggest there is a potential physiological explanation for the role of forest nutrition in the general health of western forests (Mandzak and Moore, 1994; Moore et al., 1994). Subsequently, Shaw et al. (1998) fertilized Douglas-fir seedlings with the four possible combinations of high and low N and K and found the highest P/S values in root tips of seedlings treated with the two highest K levels. This indicates that the increased mortality of Douglas-fir growing in K-poor soils (Mika and Moore, 1990; Mika et al., 1992; Moore et al., 1994) might be associated with lower P/S in their roots. When tested under field conditions in Idaho, however, a single application of N, K, or N + K did not change the incidence of Douglas-fir mortality from *Armillaria* root disease over a 5 or 10-year period (Schwandt, 2002). In addition, root P/S values were determined 1 year after treatment and were shown to be highest in the treatments receiving K, as in previous studies.

Early studies testing the impact of fertilization treatments on reducing *P. weirii*-caused mortality, or increased tree vigor to enhance resistance toward LRR, gave positive results. Survival of *P. weirii* decreased in wood blocks buried in soil with high N levels (Nelson, 1970, 1975). Mountain hemlock, *Tsuga mertensiana* [Bong.] Carr., seedlings planted in soil collected from the field and exposed to *P. weirii* inoculum under growth-room conditions expressed reduced foliar damage (yellowing, browning, or needle loss) when fertilized with N, or a nutrient solution (N, P, S), in comparison to controls that were not fertilized (Matson and Waring, 1984). The importance of tree vigor was also proposed for the disease resistance of young mountain hemlock that regenerate in canopy gaps or dieback zones of old-growth mountain hemlock created by LRR (Waring et al., 1987). The bare and young regrowth zones had higher levels of soil N, more light, and the young trees had higher vigor indexes than in the adjacent forest and reportedly would grow disease-free for 88–165 years (McCauley and Cook, 1980) in the presence of LRR inoculum sources. More recently, however, Hansen and Goheen (2000) challenged the Waring hypothesis linking tree vigor with resistance to LRR. At four study sites in Oregon, they found the extent of inoculation success and incipient decay to be the same for high and low vigor Douglas-fir and mountain hemlock. In addition, fertilization of Douglas-fir with N at 0, 336, 672 or 1345 kg N ha^{-1} had no affect on LRR-caused mortality 23–27 years after treatment at any of five study sites in Oregon and Washington (Thies and Westlind, 2005).

Extrapolating the promising results from studies of *Armillaria* root disease in mixed conifer stands conducted in the early 1990s, foresters in western Washington began considering the use of potassium fertilization in the late 1990s to alter the physiology of Douglas-fir and increase resistance to LRR. At that time there were no reports of K fertilization effects on LRR-caused mortality of Douglas-fir. In this paper, we report a study testing the hypothesis that applications of K as KCl, or K + N as urea, to a planting site will change the incidence of Douglas-fir seedling mortality caused by LRR.

2. Materials and methods

2.1. Study area

The study area was a 52.3-ha clearcut west of the Cascade Range crest near Morton, Washington (46°31′N, 122°01′W) on a 4% west-facing slope; mean elevation of 290 m. Mean annual precipitation is 150 cm. Soil in the study area is mapped as Cispus (cindery, mesic Umbric Vitrandepts) (US Department of Agriculture, 1987). The average site index for this soil is 38.72 m at 50 years; it supported a 65-year-old, naturally regenerated stand (following logging) that was predominantly Douglas-fir. The nutritional status of the soil and its uniformity across the site was not known.

2.2. Plots

Each plot was a 0.02-ha circle centered on an infected stump. Before logging, standing dead trees visible in the upper one-third of the crown layer were identified on aerial photographs and then located on the ground. A dead tree with LRR, as determined by the presence of ectotrophic mycelia typical of *P. weirii* on roots near the root collar (Thies and Sturrock, 1995), and more than 17 m from another identified tree, was tagged and mapped. Each tagged tree was felled leaving a 1.5-m-high stump to facilitate relocation; then the rest of the stand was logged. After logging, to facilitate examination for LRR, stumps were cut again near ground level and the stump top examined for stain typical of LRR (Thies and Sturrock, 1995). Stain on fresh cut stumps appear as spots or broad bands in the outer heartwood, above the point of attachment of major infected roots (Thies and Sturrock, 1995). We assumed that the total root biomass infected was proportional to the percentage of the stump circumference infected (CI). To ensure that inoculum remained undisturbed,

we avoided chopping into roots and rejected any stumps that had been damaged or moved during logging. Of the tagged trees, 44 were selected that had no logging damage and the most stain (39 stumps had a CI of 100% and five stumps had a CI > 60%). Logging slash within 9 m of each selected stump was removed to facilitate planting and observations. To reduce damage to plot stumps and to keep compaction to a minimum, slash was removed by using an excavator with a long-armed grapple bucket which allowed woody debris to be picked up and set aside with minimal soil disturbance. A 0.02-ha circular treatment plot was established and centered around the midpoint of each tagged stump. Each plot consisted of a measurement zone extending 3.05 m from the plot center and a buffer zone extending 3.05–8.02 m from the plot center.

The stumps on each plot were examined and the diameter (15 cm above the ground) and CI for those with LRR were recorded. We assumed the amount of inoculum was proportional to the infected biomass of the stump and belowground roots. A regression equation (Thies and Cunningham, 1996) was used to estimate belowground biomass of each stump: $\ln(LRB) = -4.41 + 2.41 \ln(DSH)$; where ln is the natural logarithm, LRB is the large root biomass (kg of roots 1 cm and larger in diameter), and DSH is the diameter at stump height (15 cm above mean ground level). Note that the preceding regression was based on a sampling of trees in Oregon only, as no other data were available. For each stump, an index of relative inoculum potential was calculated as follows: INOC = LRB × CI/1000; where INOC is the relative biomass of potential inoculum, and CI is the percentage of the stump top circumference showing stain or decay from LRR. Each measurement plot was rated for inoculum potential by totaling the INOC for stumps within the measurement plot and adding 25% for the roots of infected trees in the buffer zone we assumed would extend into the measurement plot. When another infected stump was within 3 m of a tagged stump the inoculum from that stump was considered part of the measurement plot. Plots were ranked in descending order of total INOC and then separated into groups of four with similar INOC levels, thus yielding 11 replicate blocks of four plots each.

2.3. Seedlings

A total of 50 Douglas-fir seedlings (2-1 bare-root) from a local seed source were planted in each plot measurement zone (within 3.05 m of the stump), and spaced about 0.8 m apart (12,000 seedlings ha^{-1}); additional seedlings were planted in the buffer zone with an intertree spacing of about 2.1 m (2200 seedlings ha^{-1}). Seedlings in the measurement zones were distinguished by a wire flag placed beside them. Seedlings were planted in January 1999 under near ideal, cool, wet planting conditions. By July 2002, seedlings were beginning to appear crowded, and each measurement zone was thinned to 25 live seedlings per plot. Thinning was based on spacing without regard to seedling size or foliar color intensity. No other management activities were conducted on the plots through fall 2005.

2.4. Fertilizer treatments

Four fertilizer treatments were randomly applied to the four plots in each block just after the seedlings were planted: no fertilizer applied (K_0N_0); 224 kg K + 0 kg N ha^{-1} (K_2N_0); 448 kg K + 0 kg N ha^{-1} (K_4N_0); and 224 kg K + 224 kg N ha^{-1} (K_2N_2). Potassium was applied as granules of KCl and N as prills of urea. The fertilizer was broadcast over the measurement and buffer zones using a cyclone-type seed spreader, with half applied by walking parallel transects across the plot and the remainder spread in a similar manner on transects perpendicular to the direction of the first lines. This application technique ensured even application.

2.5. Mortality surveys and seedling tissue samples

Mortality was surveyed on each plot measurement zone, and the roots of dead seedlings examined for evidence of LRR in the falls of 1999–2005, except for 2002 when plots were examined during the summer, before being thinned. Height of each live seedling in the measurement zones was recorded in fall 2001. To evaluate seedling response to the treatments, needles and root samples were collected at the end of the first growing season (late November 1999). Another needle sample was collected and analyzed in July 2002. One seedling at each of the four cardinal directions was selected in the treated buffer zone, and four branch tips from the current year that had been exposed to full light were clipped from the upper portion of their crowns. All branches were combined in a bag to yield one needle sample per plot. They were transported at ambient temperature to the lab where they were air-dried and the needles removed.

The root systems of the same four seedlings sampled in 1999 were removed from the soil by hand pulling at the stem base. After severing and discarding the stems we dislodged excess soil from the roots and combined the roots into one plot sample in a plastic bag. Bags were placed on ice in a cooler for transport to the laboratory, where they were stored overnight in a 7 °C coldroom. Roots were rinsed the next day to remove residual soil and then placed into clean plastic bags for storage at −36 °C. Prior to analysis the root samples were dried at 60 °C for 48 h and ground in a Wiley mill to pass a 2.0-mm screen. After thorough mixing, an aliquot of this material was ground to pass a 40-mesh screen and then redried at 60 °C for 16 h before storing in a screw-cap vial. Roots were not sampled in July 2002.

2.6. Needle analysis for N and K

Needles were sent to the Oregon State University Central Analytical Lab for analysis of N and K. This facility uses standard analytical methods for agricultural laboratories (Gavlak et al., 1994). The air-dried samples were ground, or pulverized, to pass a 40-mesh screen and subsamples removed for determination of dry matter content. About 250 mg of each sample was used to analyze for K, plus 11 other elements simultaneously using a nitric acid/hydrogen peroxide digestion (Kingston and Jassie, 1986; Sah and Miller, 1992) in conjunction with microwave heating in closed Teflon® vessels. Concentrations

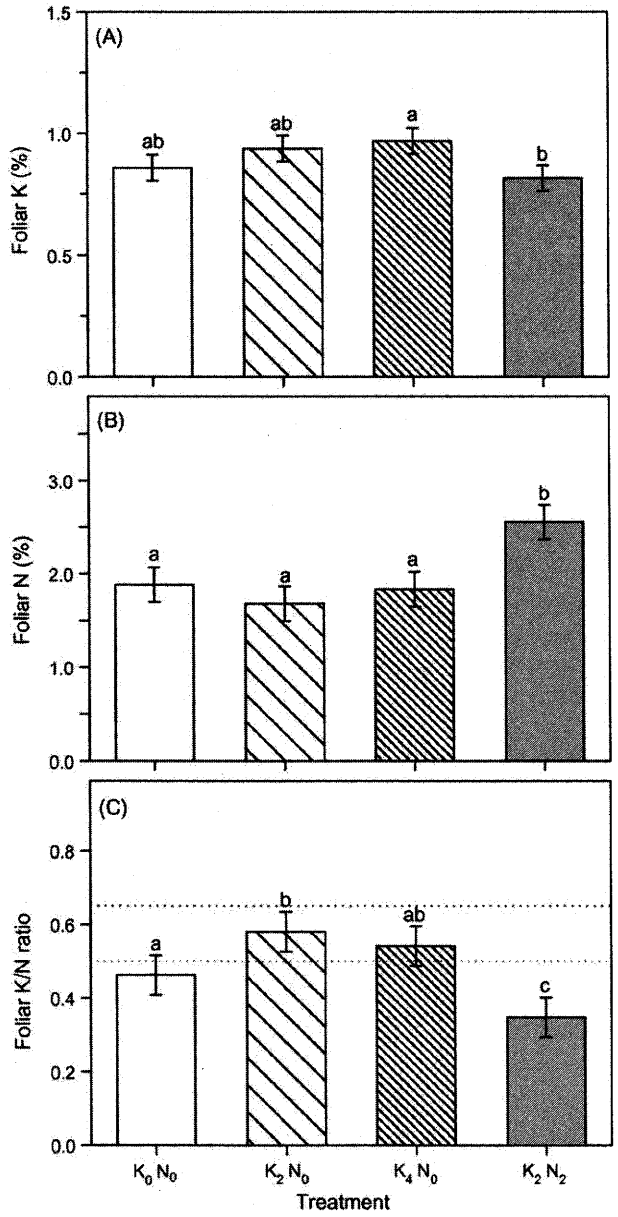

Fig. 1. The foliar concentrations of K (A), N (B), and K/N ratios (C) for Douglas-fir seedlings in the fall of 1999, one growing season after the application of fertilizer treatments. Bars represent means ± 1 S.E. Those bars with the same letter are not significantly different at $p = 0.05$. In (C), the area between the dotted lines (0.50 and 0.65) represents K/N ratios considered balanced for Douglas-fir growth (Ingestad, 1979; Mika and Moore, 1990).

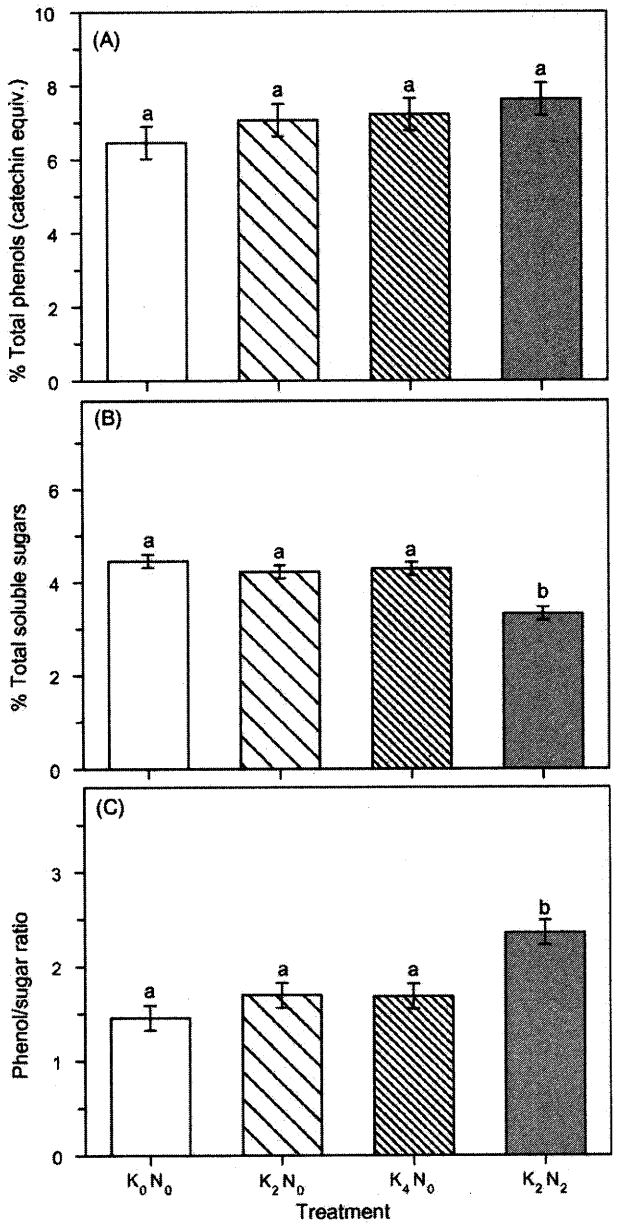

Fig. 2. The concentrations of total phenols in catechin equivalents (A), total soluble sugars (B), and P/S ratios (C) for Douglas-fir seedlings in the fall of 1999, one growing season after the application of fertilizer treatments. Bars represent means ± 1 S.E. Those bars with the same letter are not significantly different at $p = 0.05$.

of the elements in the digest were determined by atomic absorption spectrometry or inductively coupled plasma atomic emissions spectroscopy. Nitrogen was determined with about 150 mg of tissue by using a resistance furnace and a thermal conductivity detector as described by Sweeney (1989). Concentrations of all elements were calculated on a dry matter basis.

2.7. Total phenols in roots

To extract total phenols from root tissues duplicate 100-mg portions of the ground and dried root samples were weighed into 15 ml centrifuge tubes and covered with 10-ml of aqueous acetone (acetone:water, 8:2). After 16 h extraction the tubes were centrifuged (Sorvall TC6 bench top model) for 5 min at 3000 rpm, and the solvent decanted into another tube sealed for storage at room temperature. The total phenols were quantified by the Folin–Ciocalteu method described by Waterman and Mole (1994) using 0.5 ml of the extract, or a standard solution of catechin, with the quantities of reagents used scaled to our needs based on preliminary tests. Absorbance of the reaction mixture at 760 nm was measure 2.0 h ± 1 min from the start time (addition of sodium carbonate solution) with the same

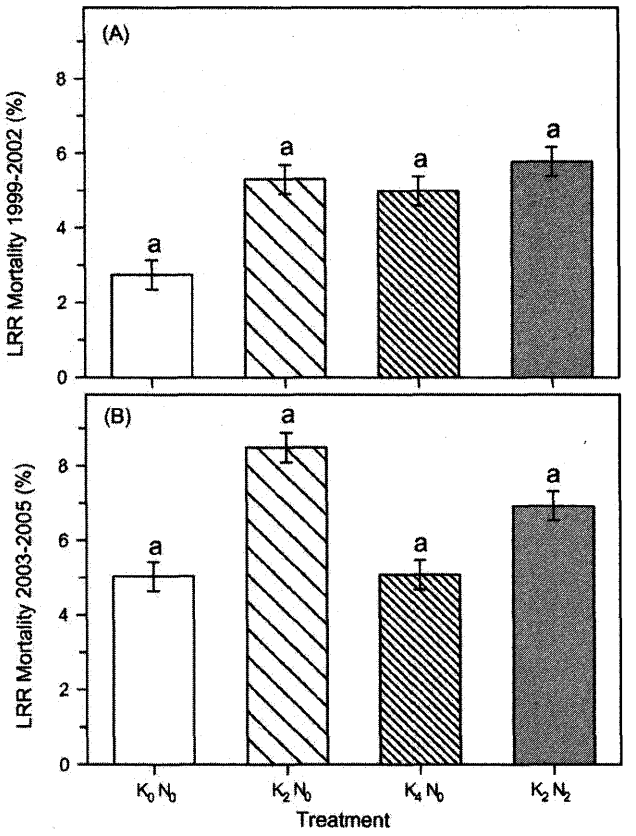

Fig. 3. The percentage of mortality in Douglas-fir seedlings from LRR from 1999 to 2000 (A) based on 50 seedlings/plot before thinning and from 2003 to 2005 (B) based on 25 seedlings/plot after thinning. Bars represent medians ± 1 S.E. Those bars with the same letter are not significantly different at $p = 0.05$.

instrument described for the soluble sugars below. A standard curve with three concentrations of (+)-catechin hydrate (approx. 10% water content) was run with each set of samples analyzed. Phenolic concentrations in catechin equivalents were calculated as a percentage of tissue dry weight (60 °C). The Folin–Ciocalteu's phenol reagent was purchased from Sigma, and the (+)-catechin hydrate standard was obtained from Fluka.

2.8. Total soluble sugars in roots

To extract total soluble sugars from root tissues, duplicate 100-mg portions of the ground and dried root samples were weighed into 15-ml centrifuge tubes and covered with 10 ml of deionized water. After 60 min, with periodic shaking, the water was filtered through coarse porosity, fast-flow filter paper and stored at 7 °C. Total soluble sugars in 200 μl of extract, incubated overnight at room temperature with invertase to hydrolyze sucrose, were measured by the colorimetric method described by Blakeney and Mutton (1980), with quantities of each reagent modified for our analysis as determined in preliminary trials. Absorbance of each reaction mixture was measured in a Shimadzu UV-visible 265FW spectrophotometer set at 415 nm. A standard curve with four concentrations of glucose was run with each set of analyzed samples. Sugar concentrations were calculated as a percentage of the tissue dry weight (60 °C). All chemicals were from Sigma, except for the sodium hydroxide from Mallinckrodt.

2.9. Data analysis

This experiment was set up and analyzed as a randomized complete block design with 11 replicates for each treatment. The concentrations of K, N, K/N ratios in needles (measured fall 1999 and summer 2002), the concentration of total phenols, total soluble sugars, and their ratios (P/S) in roots from fall 1999, the percentage of LRR-killed seedlings from 1999 to 2002 (based on 50 seedlings before thinning) and from 2003 to 2005 (based on 25 seedlings after thinning), and mean seedling height (fall 2001) for each plot were analyzed by analysis of variance with blocking to determine treatment differences. Assumptions of normality and homogeneity of variances were evaluated for all data sets prior to analysis by examining normal probability plots and plots of the residuals (observed versus predicted), respectively. The only data to require transformation were the mortality percentages where an arcsine square root transformation was used. Transformed means and their standard errors (SE) were back-transformed to medians and associated SE for presentation. The differences between means were compared by Fishers Protected LSD (with model $\alpha = 0.05$) and were considered significantly different at $p \leq 0.05$. All analyzes were conducted with S-PLUS 6.1 (Insightful, 2002).

3. Results

In fall 1999, one growing season after fertilization, needles of seedlings treated with K_2N_2 had the lowest K (Fig. 1(A)) and highest N (Fig. 1(B)) concentrations of any treatments, and thus the smallest K/N ratio (Fig. 1(C)) or greatest imbalance of these two nutrients. Seedlings treated with K alone (K_2N_0 and K_4N_0) had balanced K/N ratios. The root phenol concentrations in all seedlings treated with K were slightly higher than in the controls, but none of the differences was significant (Fig. 2(A)). Total soluble sugar concentrations in the K_2N_2 treated seedlings were significantly lower than in seedlings in all other treatments (Fig. 2(B)), resulting in the highest P/S values (Fig. 2(C)). In fall 2001, 2 years after fertilization, average seedlings heights were the same on all treatments ($p = 0.816$). In July 2002, three and one-half years after fertilizer application, there were no differences in foliar K ($p = 0.667$) or N ($p = 0.603$) levels among any treatments (data not shown).

A total of 2200 seedlings were planted, flagged, and observed in the measurement zones. Ten seedlings on six plots died from mechanical damage soon after planting. From 1999 to 2002 (before thinning) 292 seedlings died, 142 from LRR, with no differences in total or LRR caused mortality among treatments ($p = 0.329$ and 0.621, respectively, Fig. 3(A)). During the 2-year period after the plots were thinned (2003–2005) 134 seedlings died, 111 from LRR, with no differences in total or LRR caused mortality among treatments ($p = 0.810$ and 0.819, respectively, Fig. 3(B)). In no case was blocking on

INOC significant for tree mortality (at the 0.05 level) with the range of p values from 0.07 to 0.98.

4. Discussion

Seven growing seasons after fertilizing with K or K + N there were no differences in Douglas-fir seedling mortality from LRR among any of the treatments. Measurements taken one growing season after treatment showed foliar N and K concentrations in all seedlings above the amount considered adequate for Douglas-fir, but K/N for the controls and those receiving K_2N_2 were below the ratio considered an adequate balance (Mika and Moore, 1990). In addition, because of their lower sugar concentrations, roots of the K_2N_2 treated seedlings had significantly greater P/S values than any of the other treatments, and thus were expected to express greater resistance to LRR, but this did not happen in our study. These results are similar to those found by Schwandt (2002) when K or K + N was applied to Douglas-fir stands in Idaho infested with *Armillaria* root rot. He observed no differences in root bark phenolic concentrations among any treatments and much higher sugar levels in the controls. Consequently, all treatments with K or K + N had P/S values about two times greater than the control, and were predicted to be more disease resistant, but they were not. Shaw et al. (1998) found the highest P/S values in root tips of Douglas-fir seedlings receiving the highest K treatments, regardless of their accompanying N treatments. Although P/S values may correlate with the risk of infection by *Armillaria* (Entry et al., 1991a,b, 1992), the ratios measured within a year of applying a single fertilizer treatment do not seem to correlate with mortality from LRR, or *Armillaria* (Schwandt, 2002), over an extended number of years. Our study was conducted at a single site in the Cascade Range, and given that responses to fertilizer are notorious for variability among sites (Mika and Moore, 1990; Mika et al., 1992; Thies and Westlind, 2005), extrapolating these results to other geographic areas, tree species, or root pathogens should be done with caution. Consistent with previous studies (Thies and Westlind, 2005), INOC as used here to stratify treatments (block) was not effective; it proved to be a poor indicator of either future total mortality or LRR-caused mortality.

Furthermore, single applications of N fertilizer are not an effective management strategy for LRR. Thies and Westlind (2005) tested four levels of nitrogen (0, 336, 672 or 1345 kg N ha^{-1}) replicated at five sites in Oregon and Washington and found no treatment differences in Douglas-fir mortality from LRR, at 23–27 years after treatment. Lastly, Hansen and Goheen (2000) did not test fertilizer treatments, but observed that LRR inoculation success or decay in Douglas-fir and mountain hemlock roots do not correlate with tree vigor, which is an indicator of an adequate nutrient balance.

Three fertilizer studies (this study; Schwandt, 2002; Thies and Westlind, 2005) have reported no reductions in Douglas-fir mortality from root diseases at 7–27 years after applying one treatment. It seems overly optimistic to expect a single fertilizer application to change the defensive root chemistry of conifers so dramatically that they remain resistant to root pathogens over several years. Results might improve with periodic fertilization, but the cost (financial and environmental) of such treatments would need to be weighed against the level of reduced mortality. At our Washington Cascades site, we concluded that the single application of K or K + N to Douglas-fir at the rates tested were not an effective management strategy for LRR. These results, in conjunction with other studies discussed above, raise doubts regarding the value of single fertilizer treatments of Douglas-fir as a management tool for combating LRR or other root diseases.

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