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Manuscript submitted to:

Canadian Journal of Forestry

Intermountain Forest Tree Nutrition Cooperative
University of Idaho

Supplemental Report No. 3

April, 1998

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Acknowledgments: The support of the Stillinger Foundation and the Intermountain Forest Tree Nutrition Cooperative located at the University of Idaho is acknowledged and greatly appreciated.

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ABSTRACT

Chemical changes in roots of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Bessn.) Franco) seedlings were induced under optimal and deficient levels of nitrogen (N) and potassium (K). Concentrations of sugar, starch, phenolics and protein-precipitable tannins were significantly different by treatment in the roots of four-year-old Douglas-fir seedlings under varied N and K regimes. Root tip starch concentrations were significantly higher and sugar concentrations were lower in plants receiving the low-N treatments. Seedlings receiving the high N-low K treatment had significantly lower concentrations of phenolics and tannins and lower ratios of defensive compounds to carbohydrates than seedlings receiving the high potassium treatments. Samples taken from two locations on the root system show that concentrations of all storage and defensive compounds were substantially higher in the root collar than in the root tips. Due to lower within tissue variation, we recommend sampling at root tips to better detect treatment differences. This study shows that N levels affect starch concentrations in the roots, while K levels affect root phenolic and tannin concentrations.

INTRODUCTION

Concentrations of storage and secondary compounds in plant tissue depend to a considerable extent on the environment in which plants grow (Waring et al. 1985; Huber and Arny 1985). In particular, mineral nutrition influences concentrations of storage compounds such as sugars and starches and defensive compounds such as phenolics and tannins (Bryant et al. 1983; Entry et al. 1991a; Moore et al. 1994). The concentrations of these compounds and the balance among them help to determine the resistance of plants to herbivores and pathogens (Wargo 1972; Garraway 1975; Ostrofsky and Shigo 1984; Larsson et al. 1986; Mwangi et al.1990; Dudt and Shure 1994). Therefore, the levels of available nutrients such as N and K may greatly influence the ability of plants to resist disease.

A tree's ability to resist a particular kind of stress can be assessed by evaluating how easily it can mobilize carbohydrate reserves near the points of potential need (Waring and Schlesinger 1985). However, competition for photosynthate may reduce the levels of carbohydrate reserves available for mobilization in various tissues. Limited resources may also favor or disfavor production of secondary compounds like phenols and tannins (Mooney 1972; Bazzaz et al. 1987).

The shifting competition for photosynthate among compounds is often described by the carbon-nutrient balance (CNB) hypothesis (Bryant et al. 1983), which suggests that carbon-rich compounds such as phenolics and tannins are produced in relatively greater amounts when photosynthate is more available and nutrients are less available. The CNB hypothesis is an extension of the earlier growth-differentiation balance hypothesis (Loomis 1932; Herms and Mattson 1992), which suggests that growth and

differentiation compete for photosynthate. Both hypotheses address the influence of shifting pools of non-structural carbohydrates on synthesis of carbon-rich compounds, and both attempt to describe the consequences of ontogenetic shifts. We therefore examined correlations between plant biomass, phenolics, tannins, sugars and starch concentrations, as well as ratios of compounds occurring in the roots. Ratios are less likely than straight concentrations to be affected by the levels of non-structural carbohydrates.

To better estimate and understand the relationship between plant nutrition, root chemistry and plant susceptibility to disease, the effects of sampling location must also be understood. Wargo et al. (1972) found that glucose and fructose concentrations in sugar maple were higher in the outermost root wood than the inner root bark. In another study with sugar maple, Parker and Houston (1971) found that levels of sugars were higher in root bark than in root collar bark. Likewise, levels of storage and defensive compounds have been shown to vary considerably along the gradient of stem and root bark (Kelsey and Harmon 1989).

The principal objective of this study was to determine the effects of varied N and K nutrition on the chemical composition of Douglas-fir roots. A secondary objective was to evaluate two sampling locations to compare distribution, trends, and variation in chemical composition.

METHODS AND MATERIALS

Treatments

One hundred four one-year-old, containerized Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Bessn.) Franco) seedlings were planted in 2900-mL plastic containers filled with medium grade silica sand. Seedlings were grown at the University of Idaho Forest Nursery in a shade house covered by a clear, corrugated fiberglass roof from June to December for three growing seasons. To ensure similar genetic variation in experimental material, seedlings from two North Idaho Douglas-fir seed sources, collected from different locations and elevations, were distributed equally by treatment and block. Seedlings were randomly assigned to four different N and K treatments within two blocks. The solution used to supply the Douglas-fir seedlings with nutrients was adapted from Ingestad and Lund (1979) and is considered nutritionally optimal. A stock solution was formulated with levels for the macro nutrients of: N, 100; K, 65; P, 13.8; Ca, 7; Mg, 8.5 and S, 15 mg/L. The micro nutrient concentrations were:: Fe, 700; Mn, 400; B, 200; Cu, 30; Zn, 30; Cl, 30; Mo,7; and Na, 3 ppm. The nutrient stock solution was modified to meet the treatment regimes shown in Table 1. Nutrient solutions were given to plants by adding them to well water through an injection system at a ratio of 1:100. Seedlings were irrigated as needed, and 500 mL of nutrient solution was applied every four days throughout the growing season. Irrigation was reduced in late September of each year to encourage dormancy. Periodic foliar sampling was used to adjust treatments so that the N and K foliar concentrations were similar to treatment ranges observed from Douglas-fir field fertilization studies. Each treatment consisted of a 3-year nutrient regime periodically adjusted to attain target nutrient concentrations. To prevent nutrient leaching

from the foliage, irrigation water and solution was applied directly to the soil through 3.2 millimeter (inside diameter) polyethylene drip tubing with Roberts 180° medium flow Spot-Spitters®. To avoid low winter temperatures, seedlings were transferred and stored at around 0°C. Day length followed seasonal variations for Moscow, ID. (Latitude 46° 44' north).

Table 1. Nutrient treatments under which Douglas-fir seedlings were grown: low nitrogen and low potassium (nk), low nitrogen and high potassium (nK), high nitrogen and low potassium (Nk), high nitrogen and high potassium (NK). Numbers are percentages of solution concentrations developed by Ingestad and Lund (1979).

Years	Treatment	Nitrogen	Potassium
One & Three	nk	10	10
	nK	10	100
	Nk	100	10
	NK	100	100
Two	nk	25	10
	nK	25	100
	Nk	100	10
	NK	100	100

Foliar Nutrients

Douglas-fir seedlings were sampled in October after three years of growth under different N and K treatments. Seedlings and the sand in which they were grown were carefully removed from the containers, sand was gently removed from the root system, then the seedlings were put into plastic bags and stored in coolers to slow plant metabolism. Foliar nutrient samples were comprised of 26 seedlings per treatment. Seedling foliage was stored at 1°C for up to 48 hours while awaiting laboratory analysis.

In the laboratory, roots were separated from the shoots and both samples were oven-dried at 70°C for 24 hours. Afterward, needles were stripped from the stem and continued to dry at 70°C for an additional 24 hours. A sample of 2 grams representative of all the needles was taken from each seedling. Foliage was ground to a very fine consistency in a Wiley mill in preparation for chemical analysis. Foliar N concentration was determined using a standard micro-Kjeldahl procedure, which is a wet-oxidation method that converts organic and inorganic N to NH_4 for quantification. Phosphorus, K, Ca, Mg, Mn, Fe, Cu, and Zn concentrations were determined by inductively coupled plasma (ICP) emission.

Root Storage and Defensive Compound Chemistry

Fifty-two composite samples were taken from the same seedlings that were used in the foliar nutrient analysis. Twenty-six root collar bark and 26 root tip composite samples (four seedlings per composite) were collected for analysis of starch, soluble sugar, total phenols and protein-precipitable tannins. Only non-mycorrhizal long lateral living root tips were included in the samples. Roots were temporarily stored for several hours in coolers while waiting for transport from the nursery, then frozen in an ultra-cold freezer at -40°C until analyzed. In the laboratory, all samples (bark and root tips) were put in liquid nitrogen overnight, and then ground to powder in a mortar. Total phenols were determined from samples after extracting with aqueous acetone (80%), adding Folin-Ciocalteu's Reagent, and then measuring absorbances at 700 and 735 nm (Julkunen-Tiito 1985). Samples were analyzed for total soluble starch through an ethanol and perchloric acid method (Hansen and Moller 1975) and glucose was determined by adding anthrone solution for absorbance determination at 630 nm (Hansen and Moller

1975). Concentrations of glucose were measured using a standard curve established with a glucose standard (Hansen and Moller 1975). The Hansen and Moller method overestimates starch levels because carbohydrates other than starch are extracted during the process (Marshall 1986, Rose et al. 1991). Perchlorate-extractable carbohydrates were, therefore, corrected to yield starch concentrations and are expressed in their corrected form throughout this paper. Tannin levels were measured after extracting with 80% aqueous acetone loaded into an agarose plate containing bovine serum albumin, diffusion rings were measured and tannin acid determined (Sigma) (Hagerman 1987). Analysis of starch, sugar (glucose), total phenols and protein-precipitable tannins analysis were performed by the Institute of Biological Chemistry, Washington State University in Pullman, WA.

Statistical Analysis

From a population of 104 seedlings, the treatment effects on foliar nutrient concentrations and root chemistry were estimated using analysis of variance for a 2 (blocks) x 2 (seed sources) x 4 (treatments) randomized complete block design. Twenty-six seedlings per treatment were used for the foliar nutrient analysis while six root collar bark or root tip composite samples per treatment were used for the root chemistry analyses. One root collar bark sample from the Nk treatment was dropped from the analysis since starch, sugar, tannin and phenolic concentrations were all more than 2.5 standard deviations from the treatment means. Analysis of variance (PROC GLM) and differences between means by treatment for foliar nutrient and root chemistry data were determined by using the least-squares means ($\propto = 0.10$) procedure of the Statistical Analysis System (SAS Institute Inc. 1985). Correlations between plant biomass

(grams/seedling), sugar, starch, phenols and tannin concentration by root sampling locations were analyzed.

RESULTS

Foliar Nutrients

Treatment differences in foliar nutrient concentrations were detected (Table 2). Foliar N concentrations were 71% higher in the seedlings receiving the high N treatments than in seedlings receiving low N treatments. Plants receiving high N and low K were significantly lower (20%) than those of seedlings receiving the high N and high K treatment. In addition, seedlings receiving the low K treatments showed K deficiency symptoms, i.e. chlorosis and necroses along the leaf margins. In our study, significant differences in foliar potassium to nitrogen (K/N) ratios were observed only between the high N and low N treatments (Table 2).

Table 2. Nitrogen and potassium foliar nutrient concentrations collected in October after three growing seasons from Douglas-fir seedlings. Treatments are the same as in Table 1.

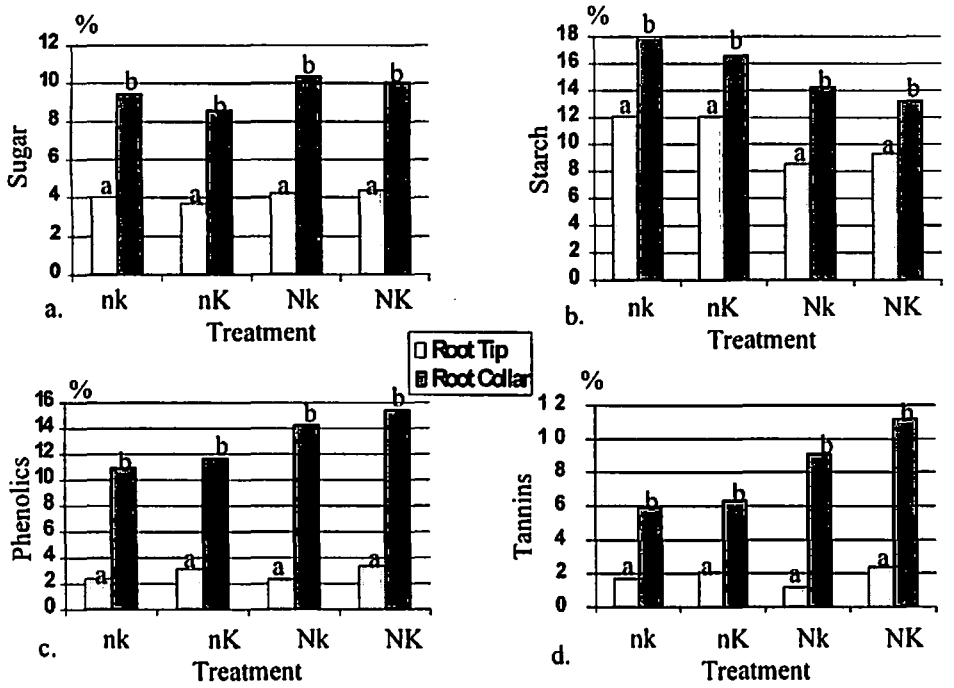
Treatment	Nitrogen (%)	Potassium (%)	Potassium/ Nitrogen
nk	1.06a	0.68a	0.67a
nK	1.13a	0.71a	0.67a
Nk	1.85b	0.59b	0.33b
NK	1.90b	0.74a	0.40b

Note: Within each column, values followed by the same letter are similar at $P \leq 0.10$.

Root Storage and Defensive Compound Chemistry

Concentrations of sugar, starch, phenolics and protein-precipitable tannins were all significantly higher at the root collar than in the root tips (Figure 1). Soluble sugar and tannin concentrations were two to three times higher in the root collar area, whereas concentrations of phenolics were up to six times higher. These results were especially pronounced in the high N-low K treatments (Nk) with phenolic and tannin levels six and seven times higher in the root collar than in the root tips, respectively (Figure 1). Overall, plants receiving the low K treatments had greater differences between the root tip and root collar for phenolic and tannin concentrations.

Figure 1. Root tip and root collar soluble sugar, starch, phenolics and protein precipitable tannin concentrations collected after three growing seasons from Douglas-fir seedlings. Treatments are the same as in Table 1. Within each treatment bars labeled by the same letter are not significantly different at $p < 0.10$.



Although sugar, starch, phenol and tannin concentrations were substantially higher in the root collar than in the root tip, the results show similar trends by treatment. Observations from the two root sampling locations were highly correlated with correlation coefficients for sugar of $r = 0.85$, starch $r = 0.79$, phenol $r = 0.93$ and tannin $r = 0.89$.

Strong correlations were observed between non-structural carbohydrates and carbon-based secondary compounds at the root collar sampling location, but not at the root tips (Table 3). As sugar concentrations increased at the root collar, so did phenolic and tannin concentrations. However, the correlations between starch and phenolic or tannin concentrations were negative. At the root tips, there were no statistically significant correlations between sugar or starch and tannin or phenolic concentrations (Table 3). Plant size, represented by total grams per seedling, showed strong positive correlation with tannin and phenolic concentrations at the root collar, but evidenced no significant relationship with these same compounds at the root tips (Table 3). Total seedling biomass was significantly ($p < 0.05$) correlated with sugar and starch concentrations at both the root collar and tips. Coefficients of determination for biomass versus sugar and starch at the root collar were .30 and .12, and at the root tips .23 and .61 respectively.

Table 3. Coefficient of determination (r^2) between total phenolics or protein precipitable tannin concentrations and soluble sugars, starch, and total seedling biomass at different root sampling locations. (** = $p < 0.01$; * = $p < 0.05$; ns = $p > 0.10$)

		Root Collar	Root Tips
Sugar	Phenolics	.32**	.00ns
	Tannins	.32**	.01ns
Starch	Phenolics	(-).32**	.01ns
	Tannins	(-).16*	.02ns
Biomass (gms./seedling)	Phenolics	.55**	(-).01ns
	Tannins	.62**	(-).03ns

Root tip chemistry was clearly affected by the treatments, except for sugar concentrations (Figure 2a). Starch concentrations were significantly lower with high N treatment levels but were unaffected by the level of K supplied (Figure 2b). Phenolic and tannin concentrations were significantly higher for the high K treatments compared to the high N low K treatment, but were unaffected by the N level supplied for a given K level (Figure 2c and 2d). The high N low K treatment produced significantly lower root tip phenolic / sugar ratios than either of the two treatments with higher levels of K supplied (Figure 3).

Figure 2. Root tip soluble sugar (a), starch (b), phenolics (c) and protein precipitable tannin (d) concentrations collected after three growing seasons from Douglas-fir seedlings. Treatments are the same as in Table 1. Bars labeled by the same letter are not significantly different at $p < 0.10$.

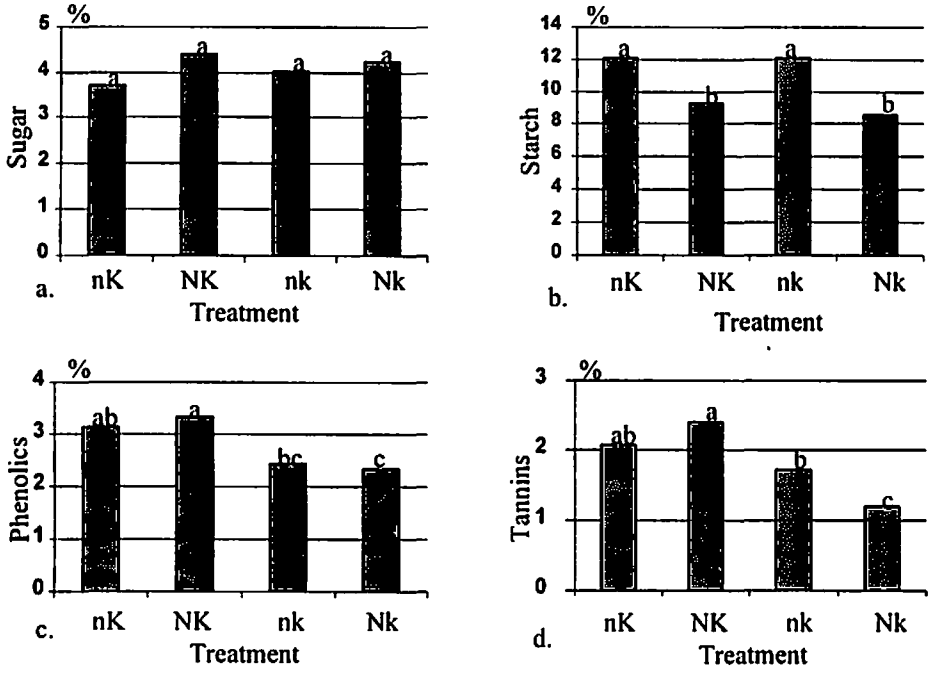
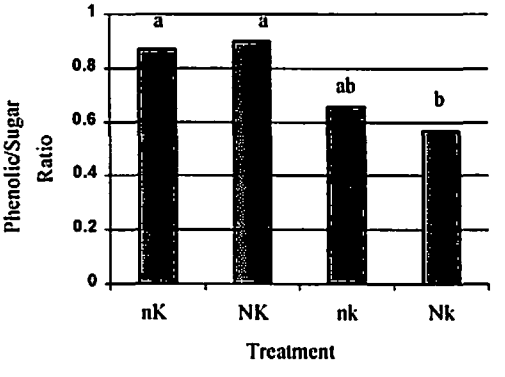


Figure 3. Root tip phenolic to sugar concentration ratios collected after three growing seasons from Douglas-fir seedlings. Treatments are the same as in Table 1. Bars labeled by the same letter are not significantly different at $p < 0.10$.



DISCUSSION

Foliar N levels for the low N treatments were well below the "adequate" threshold, whereas high N treatments were above the adequate threshold for Douglas-fir, as described by van den Driessche (1979) and Webster and Dobkowski (1983). Plants receiving high N and low K had inadequate foliar K concentrations for growth (van den Driessche 1979, Webster and Dobkowski 1983). In addition, foliar color indicated K deficiency in the needles. Seedlings that received the two high N treatments had foliar K/N ratios substantially below the 0.50 inadequate level described by Ingestad (1967; Ingestad and Lund 1979). These foliar results are similar to those of van den Driessche and Ponsford (1995) and to the N and K foliar concentrations in field-grown Douglas-fir trees, where insufficient K was associated with optimal N levels (Mika and Moore, 1991). Thus, the treatment regimes used in this study successfully created a range of nutrient status from adequate to inadequate, a situation that is desireable for observing differences in root chemistry.

Treatment effects on root chemistry were similar for both root sampling locations; however, variation not directly related to treatment was higher at the root collar. The treatments significantly affected seedling size (Shaw et al 1998), and in turn, seedling biomass significantly affected sugar and starch concentrations at both sampling locations, and phenolic and tannin concentrations at the root collar. However, seedling biomass showed no correlation with phenolic and tannin concentrations at the root tips. Seedling size differences possibly affected the mix of tissues (i.e. cambium, phloem, phellum, phelloderm and cortex) in the root collar bark samples and thus contributed to the unexplained root chemistry variation, while tissues sampled at the root tips were less

affected by seedling size and thus more uniform in composition. Therefore, we believe sampling at the root tips is preferred for experiments similar to ours, since treatment effects were pronounced and ontogenetic effects lessened.

We observed no significant correlations between sugar or starch and tannins or phenolic concentrations at the root tips. Storage carbon compounds were low in the root tips compared to the root collar. The relative lack of sugar and starch at the root tips may explain the lack of correlation with tannin or phenolic concentrations. Strong positive correlations were shown between root collar sugar concentration and tannin or phenolic concentrations. These results are similar to those of Gebauer et al. (1998) and supportive of the CNB hypothesis that secondary carbon compound synthesis depends directly on non-structural carbohydrate levels. However; root collar starch concentration was significantly negatively correlated with both tannin and phenolic concentrations. This inverse relationship is similar to that of Gebauer et al. (1998) for their lateral root sampling location; however, they showed a positive relationship between starch and tannin for their tap root sample. Perhaps the inverse relationships between starch and tannin or phenolic concentrations in our study resulted from the strong K treatment effect on tannin and phenolic concentrations.

The N and K treatments caused Douglas-fir seedlings to alter carbohydrate production and subsequent photosynthate allocation among biosynthetic pathways and seedling parts. Generally, root storage compounds such as starch were reduced in seedlings receiving the high N treatments, whereas secondary defensive compounds such as phenolics and tannins were reduced in plants receiving low K treatments. The seedlings grown with high N regimes had significantly lower levels of starch in both the

root collar and root tips than in the low N regimes. Both Wargo (1984) and Entry et al. (1991a) reported similar changes among root carbohydrates associated with N levels in conifers. In our study, phenolic and tannin levels in the root collar area were unaffected by high N treatments. However, other studies found decreased phenolic levels in leaf or needle tissue with increased N (Bryant et al. 1987, Joseph et al. 1993) or an increase in phenolic leaf concentration with decreased N (Poorter et al. 1997).

Root tip phenolic and tannin concentrations were strongly affected by the K treatments, with significant differences between the NK treatment and both low K treatments. The effect of K on phenolic and tannin levels in roots was especially pronounced for seedlings receiving the Nk treatment, which also resulted in a foliar K/N ratio well below the recommended thresholds suggested by Ingestad (1967) and Ingestad and Lund (1979). Potassium deficiencies may have affected K controlled enzymatic activities that affect carbon allocation to the shikimic acid pathway, which produces defensive carbon based compounds (Mooney, 1972). Furthermore, seedlings receiving the high N treatments were growing rapidly and may have allocated more carbon to sugar and cellulose production and less to secondary metabolites, such as phenolics and tannins (Entry et al 1991b). Penuelas and Estiarte (1998) speculated about the sources of variation that might explain different results among experiments dealing with elevated CO_2 effects on secondary carbon based compounds. They suggested that the effect of soil nutrient status could explain part of the diversity of results in the studies they reviewed. Our results suggest that K status should be particularly considered as one source of variation in studies dealing with phenolics and tannins.

Wargo (1980) and Entry et al. (1991a; 1991b) reported that increased levels of glucose enable the *Armillaria* fungus to grow more rapidly, making the fungus better able to break down phenolic compounds. The effects of excessive N on nutritional balance and plant resistance to disease have been well established. (Matson and Waring 1984; Entry et al. 1986; Ylimartimo 1991). In addition, Entry et al. (1991a, 1991b) found that the phenol to sugar ratio was related to susceptibility to *Armillaria* infection, with low ratios (ie. low phenolics and high sugars) being bad for the trees and good for the disease. In this study, high N plus low K or low K alone resulted in the lowest phenol to sugar ratios. Gebauer et al (1998) noted that the large investment of loblolly pine (*Pinus taeda L.)* into C-based secondary compounds in the roots suggested that below ground pathogens were important for growth and survival of loblolly pine. The response of these same root compounds to nutrient treatments in our study may indicate that below ground pathogens are equally important for Douglas-fir.

CONCLUSIONS

The effects of high and low N and K on the production of starch, phenolic and protein-precipitable tannin concentrations have been demonstrated in this study. Imbalances between N and K led to nutritional stress and secondary product imbalances, which may decrease resistance to disease. Sampling root tips provided better diagnostic evidence than sampling bark at the root collar primarily due to lessened ontogenetic effects. The foliar N and K levels in this study were similar to N and K concentrations in field grown plants. Therefore, these relationships between N and K nutrition and root chemistry should provide a better understanding of the relationships between mineral nutrition and tree resistance to disease in a forest environment.

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Intermountain Forest Tree Nutrition Cooperative

Supplemental Report No. 3

March 2000

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Submitted to Western Journal of Applied Forests

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ACKNOWLEDGEMENTS: The authors thank the Scotts Company and members of the Intermountain Forest Tree Nutrition Cooperative for their support. We also thank Terry Shaw and Mariann Garrison for their assistance.

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ABSTRACT

Four controlled-release fertilizers (fast release (FR), moderate release (MR), slow release (SR) and slow-release with micro-nutrients extended (ME)) were applied, at rates of 0, 5, 15 and 30 grams per seedling respectively, to ponderosa pine seedlings (*Pinus ponderosa Doug. ex Laws*) immediately after planting. Compared to the controls (0 rate), the 15 grams per seedling of FR, MR or ME fertilizer and 30 grams per seedling of SR fertilizer treatments produced significantly greater caliper growth during the first growing season and the 15 grams per seedling of ME fertilizer treatment produced significantly greater height growth during the second growing season. No significant difference in average caliper and height was found after three growing seasons. Seventy-eight, 54, 51 and 36% of total nutrients had been released from the FR, MR, SR and ME products, respectively by late August of the first growing season. By week 55 of the second growing season, the FR product had released 98% of its total nutrients and the MR, SR and ME products had released over 90% of their nutrients. Insufficient nutrient supply resulted in decreases in foliar N and P concentrations, as well as foliar B, Cu and Fe deficiency, and subsequently non-significant treatment effect on caliper and height after 3 growing seasons.

INTRODUCTION

Fertilizing seedlings at or near the time of planting to enhance seedling growth and survival is an increasingly common practice. Fertilization experiments have shown that application of soluble inorganic fertilizers in new plantations generally results in increased growth (Ballard, 1978). However, some fertilization experiments in conifer plantations also showed that soluble fertilizers increased mortality rates and did not improve early growth (White, 1960; Sutton, 1982). Increased mortality was primarily a consequence of the osmotic effect of high salt concentrations in the rooting zone. Poor seedling response to soluble fertilizers seemed related to the inability of newly planted seedling root systems to use large quantities of applied nutrients. Nutrient uptake by competing vegetation as well as the movement of the applied nutrients through the upper soil profile also contributed to poor response (Brockley, 1988).

Controlled release or organic fertilizers were used in some fertilization experiments (Arnott and Brett 1973) in order to overcome the disadvantages of soluble inorganic fertilizers. The release rate of controlled release fertilizers is determined predominately by the thickness and solubility characteristics of the coating materials as well as temperature during release. Tree growth response to controlled release fertilizers varies with nutrient formulations, release characteristics, application rates, and fertilizer placement methods (Carlson and Preisig, 1981). The three placement methods that have been commonly used with planting time fertilization are: planting hole application, adjacent application, and broadcast application. One problem with broadcast application of fertilizer is the possibility of stimulating growth of competing vegetation compared with either in-hole or adjacent placements. In New Zealand, fertilizers applied at planting are placed in a slit approximately

15 cm from the seedling to stimulate tree growth and simultaneously avoid vegetation competition (Ballard, 1978).

The success of fertilization with controlled release fertilizers depends on factors such as nutrient formulations, release characteristics, application rates, placement methods and their interaction with seedling stock type, climate and soil. Treatment effects have been measured in terms of tree growth, mortality, nutrient loss, weed competition, economical and environmental feasibility. Extensive field tests of seedling fertilization with controlled release fertilizer applied at planting are needed before appropriate prescriptions can be developed for inland Northwest forest conditions.

In 1996, a fertilization experiment using four controlled release fertilizers of various release characteristics and nutrient formulations (Table 1) was initiated at the time of planting a ponderosa pine plantation on the University of Idaho Experimental Forest. The major objective of this study was to test the effects of adjacent placement of four fertilizer products at various application rates on ponderosa pine seedling survival, growth and foliar nutrient concentration. A secondary objective was to determine the release characteristics of the fertilizer products under the environmental conditions at the experimental site.

MATERIALS AND METHODS

Site description

The experiment was located in Latah county in northern Idaho at 46° 51′ N and 116°50′ W., elevation 950 m. The study site was clearcut in 1995 and the slash burned in the spring of 1996 and is characterized by Vassar Silt Loam soil which is 1.5 m deep. The habitat type is *Abies grandis/Clitonia uniflora* (Daubenmire and Daubenmire 1968). In winter, the

average temperature is 0 °C, and the average daily minimum temperature is –4 °C. In summer, the average temperature is 17 °C, with an average daily maximum temperature of 27 °C. Located just out of the rain shadow of the Cascade Mountains, the summers begin moist and gradually turn dry by mid-July and continue mostly without appreciable rain through mid-September. October brings an increasing chance of rainfall. As autumn progresses into winter, the precipitation increases dramatically falling as either snow or rain. The total annual precipitation is 763 mm. Of this, 267 mm, or 35 percent, usually falls in April through September (Osborne and Appelgren 1996). Applying foliar active herbicide prior to planting and then twice more during the study period controlled competing vegetation.

Experimental design and treatments

A randomized complete block design was used with six blocks per treatment on the 0.425-ha experimental site. Each block included thirteen square plots of size 8 by 8 m, in which 36 trees were planted at a 1.3 by 1.3 m spacing. All ponderosa pine seedlings (160/90 container stock type) planted for this study were raised the previous year (1996) at the University of Idaho Forest Research Nursery and were planted between May 22nd and 24th, 1996. Twelve fertilization treatments, that is, 5, 15 and 30 grams of four kinds of controlled release fertilizers (Table 1), and one control (no controlled release fertilizer applied) were randomly assigned to the thirteen square plots. The ME product has the micro-nutrients outside the coating that are quickly released. The macro-nutrient release rate for the ME product is similar to the slowest release product also tested in our study. Fertilizers were

applied into a hole 15 cm (6 in.) deep and 8 cm (3 in.) away from the planting point on the up-hill side immediately after planting.

To monitor fertilizer release rate, fifteen grams of the four fertilizer products were placed into sixty 25 by 5 cm fiberglass mesh bags. The bags were labeled and randomly placed into 15 cm deep slots in the middle of the sides of individual plots. Six bags from each fertilizer product were collected every two months for two years and sent to Scotts Laboratories for analysis of nutrient release.

Field sampling and measurements

The response variables of interest were caliper (diameter at the root collar), height, survival and foliage nutrient concentrations. Seedling height and caliper were measured at planting and in late October of the 1996, 1997 and 1998 growing seasons. Relative caliper and height growth rates (RGR) were calculated for every plot by:

$$RGR = \frac{\ln Y_2 - \ln Y_1}{T_2 - T_1} \qquad (1)$$

Where Y_1 and Y_2 are the seedling's average caliper or height for each plot at two points in time (T_1 and T_2) and ln is natural logarithm. Survival was surveyed bi-weekly throughout the first growing season (1996) and was calculated for each plot as the percentage of live seedlings relative to the total number of seedlings planted. At the end of each growing season, three fascicles of needles located nearest the top bud were removed from each interior seedling of a plot. Needles were oven-dried at 70°C for 2 days and ground for chemical analysis. Analyses for the nutrients: N, P, K, Ca, Mg, B, Cu, Zn, Fe, Mn and Mo were conducted, all of which were present in the controlled-release fertilizer products. Foliar

N was determined using a standard mico-Kjeldahl procedure. Phosphorus, K, Ca, Mg, Mn, Fe, Cu and Zn were determined by inductively coupled plasma (ICP) emission with digested plant tissue. Scotts Laboratories in Allentown, PA completed the nutrient analyses.

Soil moisture and temperature at 10, 20 and 40 cm depths at six points distributed uniformly across the trial were also monitored bi-weekly throughout the first growing season to evaluate their potential impacts on seedling growth and mortality. In November of 1998, nine plots were selected systematically as sampling points for soil chemical analysis. Sample locations were selected such that they were unaffected by fertilizers placed with the seedlings. In each plot, four 30 cm deep soil cores, one from each quadrant were taken and composited for soil pH, NO_3^--N, available P, Mn, Cu, Zn, Fe, exchangeable soil K, Ca and Mg analyses. Soil pH was measured 1:1 in H_2O. Nitrate was extracted with calcium oxide and was determined using automated colorimetry. Exchangeable K, Ca and Mg (1 N ammonium acetate, pH 3.0) were analyzed by ICP spetrometry. Available P was determined on a 2-g sub-sample of soil extracted with 12 mL of Bray's solution (Bray and Kurtz, 1945). Available Mn, Zn, Cu and Fe were analyzed by atomic absorption.

Data analysis

For growth response analysis, the average caliper and height as well as the relative growth rates based on the sixteen interior seedlings from each of the 36 plots were used for detecting fertilization effects. Dunnett's multiple comparison test (Kirk 1995) was conducted to detect differences in survival, caliper and height means and growth rates between the twelve fertilization treatments and the controls. With respect to the twelve fertilization treatments (four fertilizer types by three application rates), analyses of variance were conducted on caliper and height growth and foliar nutrient concentrations respectively

to test the effects of fertilizer type and fertilizer application rate as well as their interaction on caliper and height growth and foliar nutrient concentrations of ponderosa pine seedlings. Regression of first-year caliper versus fertilization application rate was performed using a parabolic model of the form:

$$Y=a_0 + a_1 X + a_2 X^2 + \varepsilon \qquad (2)$$

Where Y is seedling first-year caliper, X is the fertilizer application rate, a_0, a_1 and a_2 are the regression parameters and ε is the random error which for the purpose of statistical inferences is assumed to be distributed normally with mean 0 and a common variance. The estimated application rate associated with maximum caliper and height was determined via differentiation of equation (2) as follows:

$$\text{estimated application rate} = - \hat{a}_1/2\,\hat{a}_2 \qquad (3)$$

All statistical computations were performed using the General Linear Model (GLM) procedure of SAS (SAS, 1995).

RESULTS

Soil nutrient concentrations, moisture and temperature regimes

Measured soil chemical and physical properties important for tree growth are shown in Table 2 and Figure 1. Soil nitrate and Cu concentrations at the experimental site were very low. The experimental site experienced a very dry period from mid-July until late September. Soil moistures between 11-40 cm deep during this period were below 25%, which was disadvantageous for nutrient release and tree growth. Soil temperature at the 3 sampling depths remained at about 10° C throughout the sampling period.

Caliper and height

Total caliper and height as well as periodic growth for both attributes were analyzed. Managers are particularly interested in total seedling size, while analysis of growth rates allows better interpretation and explanation of results. Caliper and height of ponderosa pine seedlings following the fertilization treatments are shown in Figures 2 and 3, respectively. Significant fertilization effect on caliper growth was detected at the end of the first growing season (Table 3). Fifteen grams of FR, MR or ME fertilizer and 30 grams of SR fertilizer produced greater caliper growth rate than did the controls. At the end of the second and third growing seasons, no significant fertilization effect on caliper growth was found (Table 3). Most fertilization treatments had lower caliper growth rates than the controls during the second two years, although the differences were not statistically significant. Regression of first-year caliper versus fertilizer application rate for each fertilizer type separately and then solving equation (3) showed that 18.7, 17.9, and 14.7 grams per seedling rate for the FR, MR, and ME fertilizers respectively produced maximum caliper response (Table 4). The quadratic term in equation (3) was not significant for the SR fertilizer and a linear model fit the data better. This result indicates that maximum caliper response to the SR fertilizer did not occur within the range of fertilization rates tested in this study.

Unlike caliper, no fertilization effect on height growth or total height was found at the end of the first growing season (Table 3 and Figure 3). At the end of the second growing season, fifteen grams of ME fertilizer produced significantly greater height growth rate than did the controls. Moreover, all fertilization treatments had greater height growth during the second growing season than the controls even though the differences were not statistically significant (Table 3). During the third growing season, no fertilization effect on height

growth was found. After three years, there were no significant treatment effects on total caliper or height (Figure 3).

Mortality

Based on ANOVA results, there was no significant fertilization effect on the first-year mortality of ponderosa pine seedlings. The mortality for the controls was 4.2% and ranged from 1 to 13% for the fertilization treatments. However, a trend in mortality by dosage was evident, higher dosages resulted in higher mortality (Figure 4). During the first growing season, dead (brown) needle tips were observed for ponderosa pine seedlings treated with ME fertilizer, and the frequency of foliar damage was higher and symptoms more severe with higher dosages. No dead needle tips were observed on new growth in the second growing season. No fertilization effect was detected on second and third-year ponderosa pine mortality.

Foliar nutrient concentrations

Analyses of variance for individual nutrients showed that the significance for the first growing season was attributable to foliar K ($p=0.0035$), Ca ($p=0.0041$), Mg ($p=0.0007$), B ($p=0.0001$) and Mn ($p=0.0001$). Dunnett's multiple comparisons indicated that the 30 grams of SR fertilizer treatment resulted in significantly lower foliar K; the 15 and 30 grams of FR fertilizer treatments and the 30 grams of SR or ME fertilizer treatments resulted in significantly higher foliar Ca; the 5 and 30 grams of FR fertilizer treatments resulted in significantly lower foliar Mg; all three rates of ME fertilizer caused significantly higher foliar B; and finally, the 15 grams of ME fertilizer resulted in significantly higher foliar Mn than the controls at the end of the first growing season (Tables 5 and 6).

Foliar B, Cu and Fe were deficient for most or all of the fertilization treatments based on the critical values suggested by Powers 1983, Powers 1985, and Boyer 1984 (unpublished). First year foliar B concentrations of ponderosa pine seedlings were extraordinarily increased by the ME fertilizer and reached concentrations over 150 ppm (Table 6).

Pair-wise comparisons between fertilizer types and application rates for each year were also made using Dunnett's multiple comparison test. Foliar N, P, B and Zn concentrations across the experimental site decreased from 1996 to 1998 (Tables 5 and 6). The decrease over all years was statistically significant for foliar N concentration ($\alpha = 0.05$). For foliar P and B concentrations, only the differences between the first and second years were significant. For foliar Zn concentration, the difference between the second and third years was significant. Foliar Ca and Cu concentrations significantly decreased from the first to second growing season and then increased from the second to third growing season. Foliar Fe concentration was not significantly different over the years. Third year foliar K concentration was significantly lower than the first and second years. Foliar Mg concentration increased significantly each year for most treatments. Foliar Mn concentration was not significantly different between the first and second years, but was significantly different the third year.

Fertilizer nutrient release

Over the period from June 10 to August 26 1996, approximately 78, 54, 51 and 36 percent of total nutrients had been released from the FR, MR, SR and ME fertilizers, respectively. By October 26 1996, the nutrients released from the FR, MR, SR and ME fertilizers on average amounted to 86, 70, 55 and 39 percent of total nutrients. By July 8th

1997 (the 55th week after placement), the FR fertilizer had released 98% of its total nutrients, and MR, SR and ME fertilizers had released 90 % of their nutrients (Figure 5).

DISCUSSION

Response of planted seedlings to fertilization depends on many factors such as tree species, seedling quality, stock type, site characteristics, site preparation, fertilizer source, placement method, and application season and rate. In this study, field mortality was not significantly influenced by fertilization; however, a trend of increasing mortality with increasing fertilizer application rates was observed. Survival was good in our study regardless of treatment.

Low foliar N, P, and K concentrations may be major reasons for lack of response for third-year seedling caliper and height. Most fertilization treatments slightly increased foliar N concentration for the first year, but not significantly as compared to the control (Table 5). Foliar K concentrations were generally less after one growing season following fertilization, although these differences were not significant in subsequent years. There were no differences in foliar N and P concentrations between fertilization treatments and the control in the second and third years. Decrease in foliar N and P concentrations over time reflected growth dilution and probable insufficient N and P nutrition. The importance of foliar N levels to growth was also supported by the significant first-year caliper growth rates of ponderosa pine seedlings treated with 15 grams of the FR, MR and ME fertilizers and 30 grams of the SR fertilizer since these treatments also produced elevated foliar N concentrations the first year. Based on product release rates (Figure 5), available nutrients from the 15 grams treatments could approximately equal those provided from 30 grams of

SR fertilizer. Likewise with the subsequent decrease of foliar N, as well as foliar P concentrations, no significant caliper growth response was found for the second and third years.

Deficiencies in foliar concentrations of Cu, Fe and B could also explain the lack of treatment response during the last two years of the study. Foliar Fe concentrations were far below the critical value of 50 ppm. Although the ME fertilizer resulted in extraordinarily high foliar B concentration at the end of the first year, other treatments had lower foliar B concentrations which were distributed around the critical value of 20 ppm. One potential explanation for the observed results could be P-induced micro-nutrient disorders (such as Cu and Zn deficiency) as reported by Teng and Timmer (1990). However, in our study, Cu, Fe and B deficiency was probably not induced by N and P, since foliar Cu, Fe and B concentrations did not change with foliar N and P concentrations over time. Furthermore, foliar Cu, Fe and B deficiency also occurred for the controls (no fertilizer added) and may have simply been caused by low soil availability. The fertilizer products apparently did not contain sufficient amounts of these micro-nutrients to alleviate the inherent deficiencies.

Fertilized seedlings were about the same height as non-fertilized seedlings at the end of the first growing season (Figure 3). This non-significant height growth response for the first year was expected since first-year height growth is mainly determined by seedling growing conditions of the previous year, in this case, a greenhouse environment prior to fertilization. For the second year, seedlings treated with 5 and 15 grams of ME fertilizer were relatively taller than other treatments (Figure 3). The 15 grams of ME fertilizer treatment produced significantly greater height growth rate than did the controls (Table 3), and by the end of the third growing season, produced seedlings taller than any other treatments (85 cm). This was

likely attributable to the nutrient release characteristics of the ME fertilizer, which was slower than the other products. The FR and ME fertilizers were better than the MR and SR fertilizers based on the final height and caliper of ponderosa pine seedlings. The advantage of the FR fertilizer was faster first-year seedling caliper growth, while the ME fertilizer resulted in a longer duration of caliper and height growth response.

Growth response of ponderosa pine seedlings also varied with application rate. Both caliper and relative caliper growth rate increased with application rate from 5 to 15 grams and then decreased from 15 to 30 grams, particularly for the first year. At 30 grams per tree of ME fertilizer, toxicity symptoms as characterized by burned needle tips, appeared. Foliar nutrient analysis indicated that this was caused by the extraordinarily high foliar B concentration. Caliper growth response for the three application rates, along with the B toxicity at 30 grams of the ME fertilizer, suggested that an "optimum" application rate was located between 5 and 30 grams. Parabolic regression of first-year caliper growth and application rates for each fertilizer indicated that 18.7, 17.9 and 14.7 grams per tree would achieve maximum caliper for the FR, MR and ME fertilizers respectively. For the SR fertilizer, however, the estimated application rate for maximum caliper growth did not occur within the range of actual application rates for our experiment, but this result accurately reflects the gently increasing growth trend for the three application rates for this product. Additional application rates should be tested in future work with all fertilizers to derive a better estimate of the rate that produces maximum caliper growth. Optimum application rate is probably best represented by a range that depends on factors such as climate, habitat, stock type, seedling quality, and placement method.

Soil moisture conditions at the experimental site, coupled with nutrient release characteristics of the fertilizers, also contributed to the non-significant caliper and height growth over the three-year period. During the long dry summer (usually from mid-July to the end of September), lower soil moisture limited nutrient release. Furthermore, the long heavy snow-covered winter (from week 24 to week 37) caused substantial nutrient release, particularly from the ME and SR fertilizers, while trees were in dormancy. Thus, the nutrients may have leached lower in the soil profile and became unavailable to the seedling root systems.

CONCLUSIONS

None of the fertilizer product/application rate combinations tested in our study proved to be effective treatments for increasing ponderosa pine seedling size after 3 years. However, our results do indicate some important areas for future research and development efforts. The lack of response was caused by limited nutrient supplies available to sustain growth response past the first growing season. Nutrient limitations were clearly evident in the continued decline of N and P foliar concentrations over the study period, as well as by low B, Cu, and Fe foliar concentrations. We recommend product development efforts to extend the nutrient release period since by early in the second growing season the FR fertilizer had released 98% of its nutrients and the MR, SR and ME fertilizers had released over 90% of their nutrients. The proportion of micro-nutrients included in the blend should also be increased because foliar B, Cu, and Fe concentrations were deficient for most fertilizer treatments. Insufficient nutrient supply for the second and third year was the major factor that caused foliar N and P concentrations to decrease and subsequently produced non-significant growth response of ponderosa pine.

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Table 1. Macro and micro-nutrients, as percent by weight, provided by four controlled release fertilizers used in the ponderosa pine seedling experiment.

Nutrient	Controlled-release fertilizer			
	Fast release (FR)	Moderate release (MR)	Slow release (SR)	Slow-release with micronutrients extended (ME)
N	15	16	15	14
P (P_2O_5)	10	8	8	7
K (K_2O)	12	12	11	10
Ca	1.5	1.5	1.5	1.5
Mg	1	1	1	1
B	0.02	0.02	0.02	0.02
Cu	0.05	0.05	0.05	0.05
Zn	0.05	0.05	0.05	0.05
Fe	0.4	0.4	0.4	0.4
Mn	0.1	0.1	0.1	0.1
Mo	0.001	0.001	0.001	0.001

Table 2. Chemical analysis of soil samples collected from 0-30 cm at the experimental site.

Attributes	Mean ± standard deviation	Coefficient of variation (%)
Cation exchangable capacity (CEC) (cmol/kg)	10.7 ± 1.1	10.1
PH	6.2 ± 0.4	7.0
NO_3^- -N (ppm)	3.0 ± 1.9	64.7
Available P (ppm)	54.9 ± 24.1	43.9
Exchangeable K (ppm)	150.1 ± 61.9	41.3
Exchangeable Ca (ppm)	1345.7 ± 251.0	18.7
Exchangeable Mg (ppm)	110.3 ± 19.8	18.0
Available Mn (ppm)	9.3 ± 3.9	42.0
Available Cu (ppm)	0.46 ± 0.13	28.3
Available Zn (ppm)	1.66 ± 0.37	22.3
Available Fe (ppm)	92.0 ± 40.8	44.3

Table 3. Relative caliper and height growth rate of ponderosa pine seedlings for the first three years under various fertilization treatments at the experimental site ('+' indicates the treatments that are significantly different from the controls (p=0.05)).

Treatment		1996		1997		1998	
Fertilizer	Dosage (g)	Relative caliper growth (%)	Relative height growth (%)	Relative caliper growth (%)	Relative height growth (%)	Relative caliper growth (%)	Relative height growth (%)
Control	0	49.0	49.3	76.3	44.3	44.3	53.4
FR	5	60.3	52.6	70.6	52.4	40.2	55.8
	15	64.6 +	50.3	64.7	54.5	47.7	54.5
	30	61.8	51.8	72.2	50.9	38.7	60.2
MR	5	63.4 +	48.4	73.3	49.7	40.9	55.4
	15	63.8 +	45.2	70.2	56.7	42.4	50.4
	30	61.1	50.2	65.3	47.1	34.8	39.5
SR	5	56.6	47.0	75.1	49.9	48.4	56.1
	15	61.2	50.5	68.6	45.1	39.1	51.8
	30	65.6 +	44.9	69.2	47.6	37.5	55.9
ME	5	60.2	50.8	78.3	58.9	45.3	55.7
	15	64.4 +	48.3	77.3	65.0 +	44.8	59.6
	30	52.1	45.6	70.1	48.1	44.3	56.1

Table 4. Regression summary of caliper response of planted "160/90" ponderosa pine seedlings at the end of the first growing season versus fertilizer application rate (equation 2).

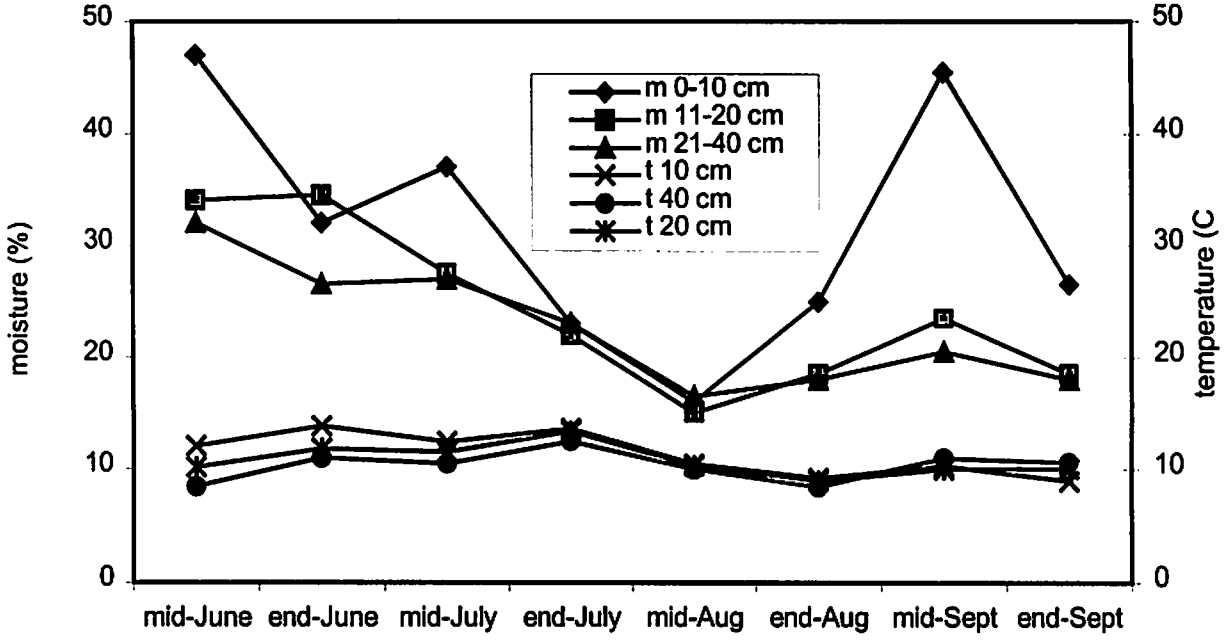
Fertilizer	Parameter	Estimate	Std. Error	Model R^2	Pr>F	Max. Rate ($\hat{a}_1/ 2\hat{a}_2$)
FR	$\hat{a}_0$	6.2533	0.2246	0.36	0.0137	18.7
	$\hat{a}_1$	0.1492	0.0509			
	$\hat{a}_2$	-0.0040	0.0016			
MR	$\hat{a}_0$	6.3170	0.2303	0.32	0.0483	17.9
	$\hat{a}_1$	0.1216	0.0478			
	$\hat{a}_2$	-0.0034	0.0015			
SR	$\hat{a}_0$	6.2816	0.162	0.31	0.0058	----
	$\hat{a}_1$	0.0431	0.031			
	$\hat{a}_2$	------	------			
ME	$\hat{a}_0$	6.2686	0.2576	0.28	0.0471	14.7
	$\hat{a}_1$	0.2300	0.0953			
	$\hat{a}_2$	-0.0076	0.0030			

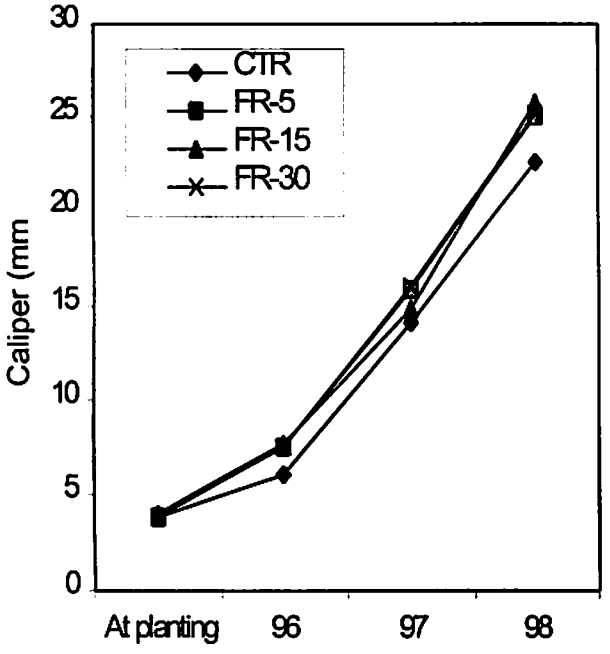
Table 5. Means of ponderosa pine seedling foliar macronutrient concentrations for various fertilization treatments for three years. ('+' or '-' indicate treatments significantly higher or lower than the control. FR= fast release; MR= moderate release; SR= slow release; ME= slow release minors extended; Three doses are 5, 15 and 30 grams per seedling).

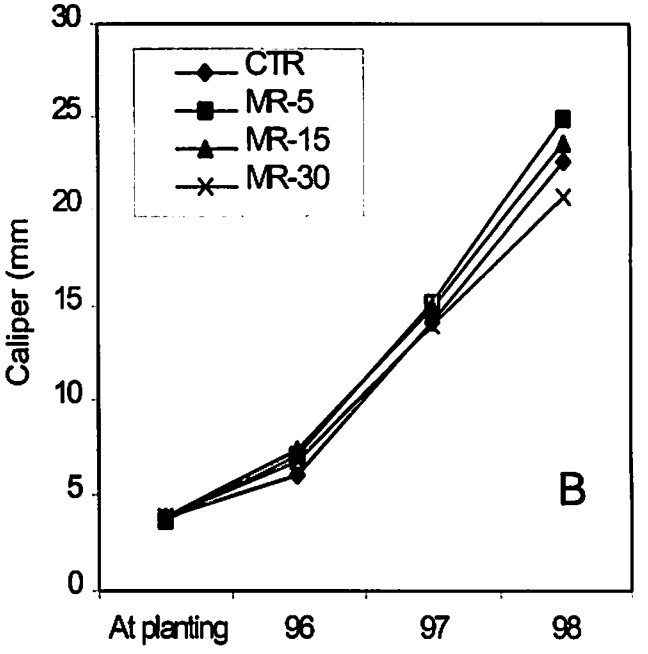
Treatment	Year	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
CTR	96	1.92	0.19	0.66	0.20	0.11
	97	1.54	0.16	0.68	0.20	0.12
	98	1.46	0.15	0.57	0.26	0.13
FR-5	96	1.92	0.19	0.63	0.21	0.10 -
	97	1.43	0.15	0.63	0.19	0.11
	98	1.33	0.15	0.59	0.23	0.12
FR-15	96	1.89	0.18	0.61 -	0.25 +	0.10 -
	97	1.54	0.17	0.64	0.23	0.12
	98	1.41	0.16	0.59	0.25	0.12
FR-30	96	2.04	0.18	0.62	0.26 +	0.09 -
	97	1.47	0.16	0.62	0.20	0.11
	98	1.42	0.16	0.59	0.27	0.13
MR-5	96	2.01	0.19	0.61 -	0.22	0.11
	97	1.45	0.15	0.67	0.21	0.12
	98	1.49	0.16	0.59	0.27	0.13
MR-15	96	1.99	0.19	0.61 -	0.24 +	0.10
	97	1.57	0.17	0.59	0.23	0.12
	98	1.33	0.15	0.61	0.25	0.13
MR-30	96	1.99	0.18	0.59 -	0.22	0.10
	97	1.52	0.17	0.71	0.18	0.11
	98	1.49	0.16	0.58	0.23	0.12
SR-5	96	1.99	0.19	0.64	0.21	0.11
	97	1.42	0.16	0.64	0.20	0.13
	98	1.35	0.16	0.61	0.25	0.13
SR-15	96	1.99	0.18	0.60 -	0.22	0.11
	97	1.46	0.15	0.65	0.20	0.12
	98	1.37	0.15	0.55	0.26	0.13
SR-30	96	1.99	0.18	0.59 -	0.25 +	0.11
	97	1.59	0.16	0.61	0.20	0.12
	98	1.39	0.15	0.54	0.27	0.13
ME-5	96	1.96	0.19	0.66	0.21	0.10 -
	97	1.47	0.16	0.66	0.20	0.11 -
	98	1.35	0.15	0.58	0.24	0.12
ME-15	96	1.89	0.18	0.66	0.21	0.10
	97	1.43	0.15	0.62	0.22	0.12
	98	1.44	0.15	0.60	0.23	0.11
ME-30	96	1.99	0.18	0.66	0.25 +	0.10
	97	1.42	0.16	0.68	0.18	0.10
	98	1.30	0.15	0.56	0.21	0.12
Critical Value		1.10	0.08	0.48	0.05	0.05

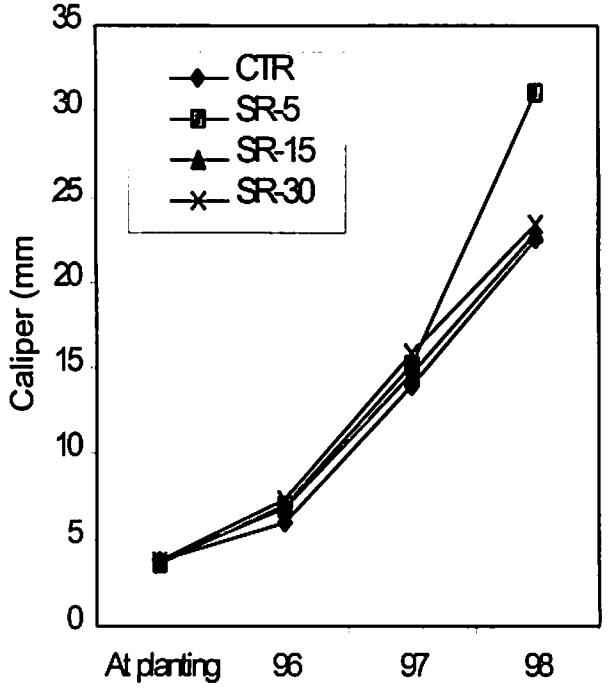
Table 6. Means of ponderosa pine seedling foliar micronutrient concentrations for various fertilization treatments for three years. ('+' or '-' indicate treatments that were significantly higher or lower than the control. FR= fast release; MR= moderate release; SR= slow release; ME= slow release minors extended; Three doses are 5, 15 and 30 grams per seedling).

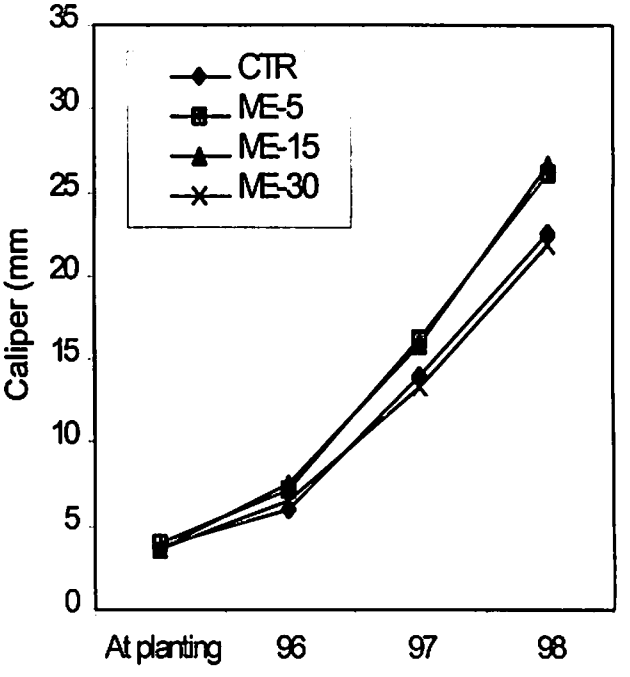
Treatment	Year	B (ppm)	Cu (ppm)	Zn (ppm)	Fe (ppm)	Mn (ppm)
CTR	96	18	3.1	73	26	109
	97	25	2.5	53	25	107
	98	14	2.8	44	26	124
FR-5	96	21	3.2	77	26	107
	97	27	2.2	84	25	119
	98	13	2.6	44	26	203 +
FR-15	96	19	3.0	70	23	104
	97	22	2.2	69	24	130
	98	15	2.6	39	25	137
FR-30	96	22	3.1	49	24	109
	97	34	2.2	45	23	119
	98	16	3.3	48	28	259 +
MR-5	96	22	3.3	104	26	117
	97	27	2.4	50	26	123
	98	13	2.6	45	26	150
MR-15	96	19	3.1	96	24	112
	97	23	2.5	110	27	116
	98	14	2.7	42	26	133
MR-30	96	19	2.7	54	22	108
	97	19	2.2	38	24	113
	98	14	2.6	38	24	141
SR-5	96	22	3.3	58	25	113
	97	26	2.5	59	25	120
	98	15	2.6	41	24	126
SR-15	96	19	3.4	50	25	109
	97	25	2.3	67	25	121
	98	14	2.3	39	24	144
SR-30	96	21	3.1	85	25	105
	97	23	2.3	57	26	116
	98	15	2.5	42	25	182 +
ME-5	96	157	3.0	72	24	126
	97	25	2.5	47	25	118
	98	15	2.8	40	24	147
ME-15	96	225 +	2.7	51	24	157 +
	97	30	2.2	61	23	126
	98	18	2.7	40	27	146
ME-30	96	284 +	2.9	63	23	130 +
	97	38	2.3	65	27	119
	98	17	2.2	32	24	133
Critical Value		20	3.0	30	50	60

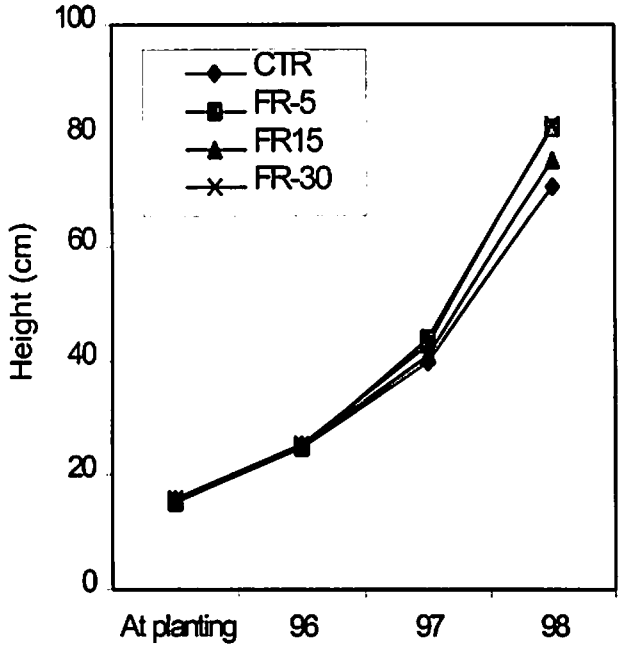

50
40
30
20
10
0
moisture (%)
temperature (C
m 0-10 cm
m 11-20 cm
m 21-40 cm
t 10 cm
t 40 cm
t 20 cm
mid-June
end-June
mid-July
end-July
mid-Aug
end-Aug
mid-Sept
end-Sept

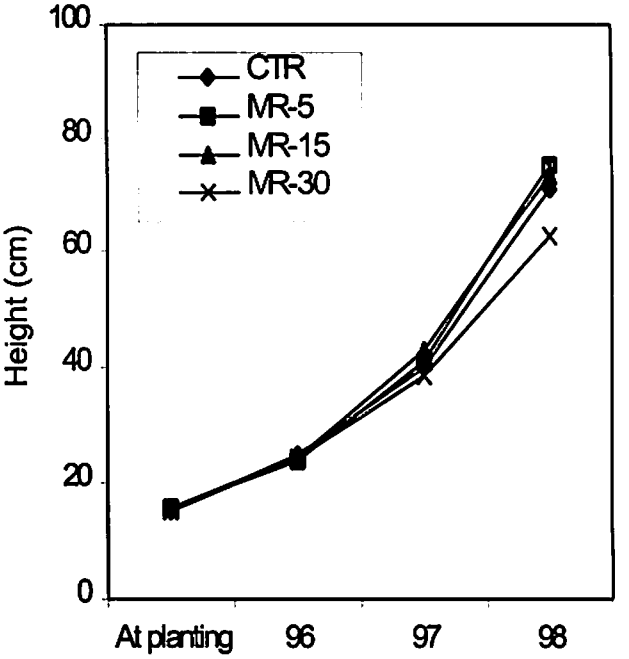

CTR
FR-5
FR-15
FR-30
Caliper (mm
0
5
10
15
20
25
30
At planting
96
97
98

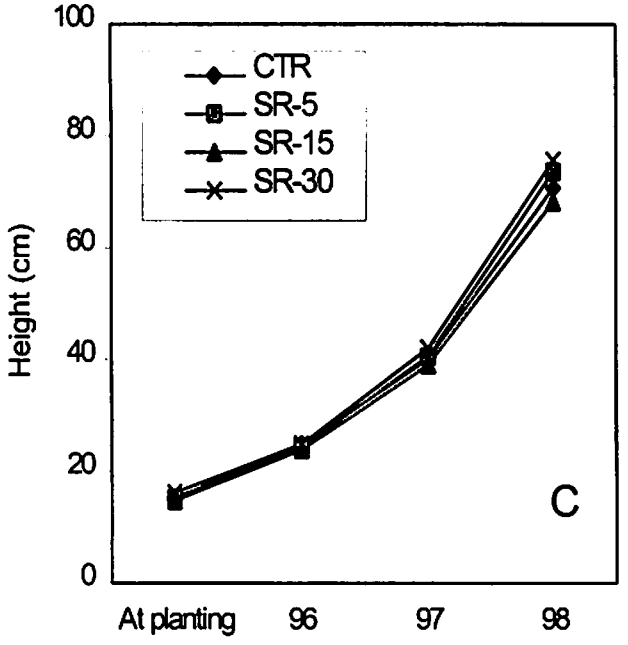

CTR
MR-5
MR-15
MR-30
Caliper (mm
0
5
10
15
20
25
30
At planting
96
97
98
B

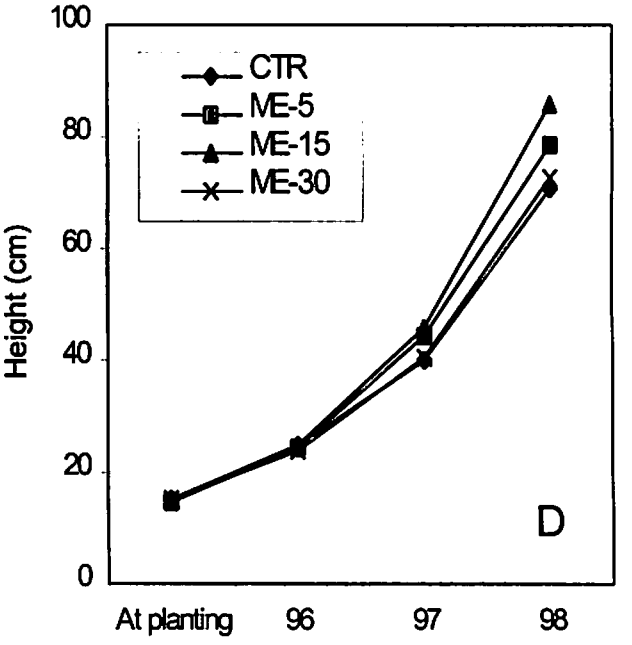

CTR
SR-5
SR-15
SR-30
Caliper (mm
0
5
10
15
20
25
30
35
At planting
96
97
98

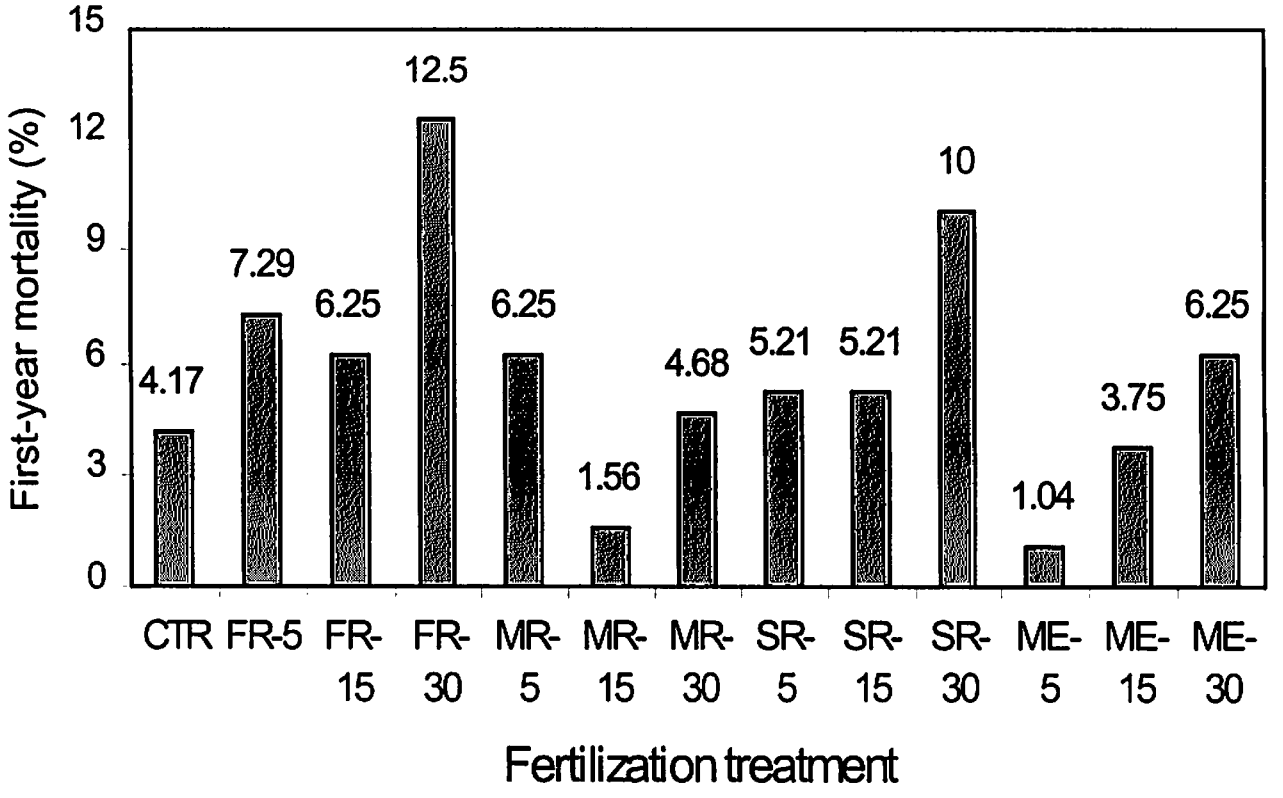

CTR
ME-5
ME-15
ME-30
Caliper (mm
0
5
10
15
20
25
30
35
At planting
96
97
98


100
80
60
40
20
0
Height (cm)
CTR
FR-5
FR15
FR-30
At planting
96
97
98


100
80
60
40
20
0
Height (cm)
CTR
MR-5
MR-15
MR-30
At planting
96
97
98


100
80
60
40
20
0
Height (cm)
CTR
SR-5
SR-15
SR-30
C
At planting
96
97
98


100
80
60
40
20
0
Height (cm)
CTR
ME-5
ME-15
ME-30
D
At planting
96
97
98


First-year mortality (%)
15
12
9
6
3
0
4.17
7.29
6.25
12.5
6.25
1.56
4.68
5.21
5.21
10
1.04
3.75
6.25
CTR
FR-5
FR-15
FR-30
MR-5
MR-15
MR-30
SR-5
SR-15
SR-30
ME-5
ME-15
ME-30
Fertilization treatment

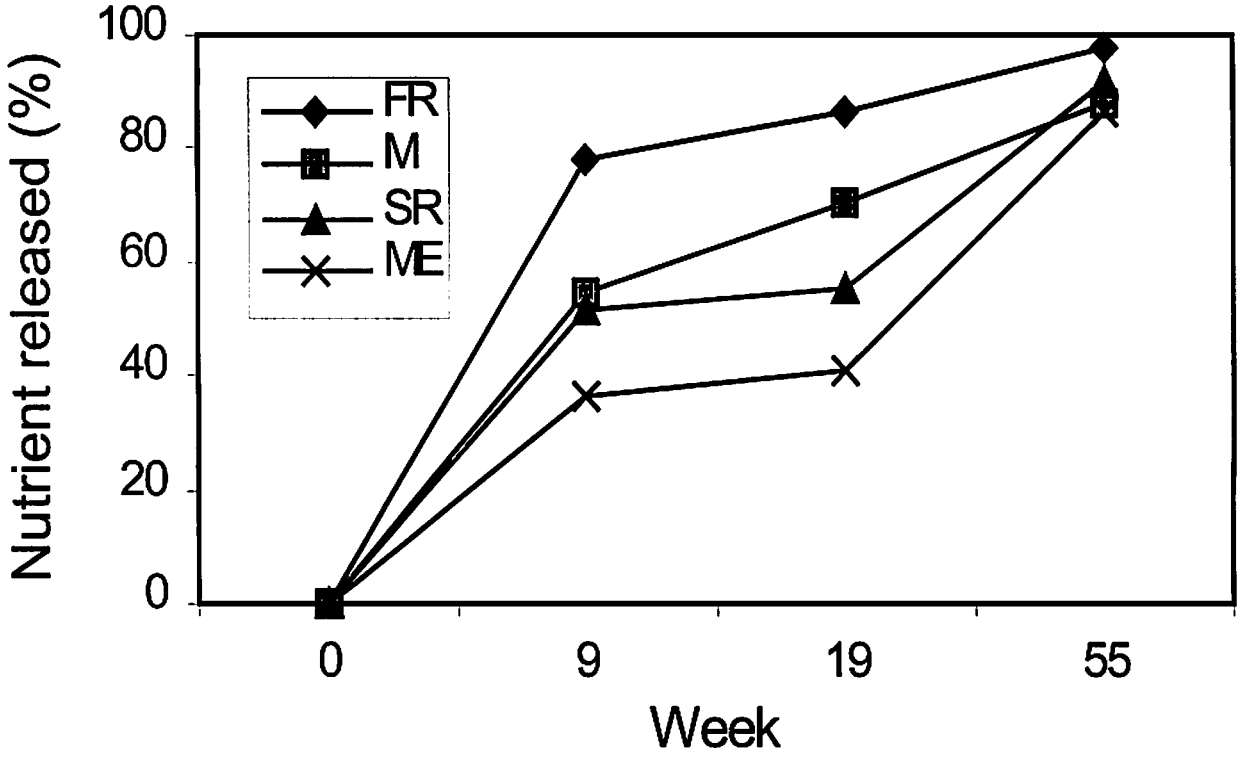

Nutrient released (%)
100
80
60
40
20
0
FR
M
SR
ME
0
9
19
55
Week

Figure 1. Observed soil moisture and temperature by Julian date at the experimental site in 1997 measured at three depths in the soil profile.

m---moisture(%) t---temperature (°C)

Figure 2. Caliper growth of ponderosa pine seedlings under various fertilization treatments at the experimental site for the first three years. FR= fast release, MR= moderate release, SR= slow release, ME= slow release with micro-nutrients extended, CTR= the controls (no fertilizer added), and 5, 15 and 30 = grams of fertilizer applied per tree.

Figure 3. Height growth of ponderosa pine seedlings under various fertilization treatments at the experimental site for the first three years. FR= fast release, MR= moderate release, SR= slow release, ME= slow release with micro-nutrients extended, CTR= the controls (no fertilizer added), and 5, 15 and 30 = grams of fertilizer applied per tree.

Figure 4. First-year mortality of ponderosa pine seedlings under various fertilization treatments at the experimental site.

Figure 5. Nutrient release characteristics of four controlled release fertilizers at the experimental site based on the fiberglass bag method.