Foliar nutrient and growth response of mixed-conifer stands on the Okanogan and Umatilla National Forests to three fertilization treatments

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Introduction

This paper summarizes results from two studies evaluating nutrient uptake in mixed conifer stands following fertilization with three nutrient combinations. The studies were conducted in northeastern Oregon and in central Washington by the Intermountain Forest Tree Nutrition Cooperative (IFTNC) in cooperation with the Umatilla and Okanogan National Forests. Four tree species were evaluated for nutrient uptake: *Pseudotsuga menzeisii* (Douglas-fir), *Abies grandis* (grand fir), *Pinus contorta* (lodgepole pine), and *Pinus ponderosa* (ponderosa pine). The fertilization treatments were nitrogen (N), nitrogen with potassium (K), and nitrogen with sulfur (S). One intent of the research was to determine whether fertilizing these stands would help hasten the rotation and bring them into production sooner by increasing growth rates and decreasing mortality rates. Another objective was to examine how various species respond to fertilization when growing together in a mixture in the same stand. Most previous fertilization trials have been conducted in relatively pure, single species stands and involved only nitrogen.

Methods

Study Area

A total of sixteen sites were established, eight each on the Umatilla (northeastern Oregon) and Okanogan (central Washington) National Forests. The stands ranged in age from 11-40 years old at the time of fertilization, with the exception one Okanogan site, which was about 70 years old. All were second growth stands, some were naturally regenerated and some planted. Foliage samples were collected from one to two species per site, based on abundance and distribution throughout the stand. Elevations ranged from 885 to 1675 meters above sea level. Vegetation series (Johnson and Clausnitzer 1992, Williams and Lillybridge 1983) included subalpine fir (ABLA), Douglas-fir (PSME), and grand fir (ABGR). Basaltic, granitic and some glacial till parent materials were represented. Elevation, vegetation series, parent material and species studied are provided for each study site in Table 1.

Table 1. Site characteristics for sixteen mixed conifer study sites located on the Umatilla National Forest in northeast Oregon and southeast Washington and the Okanogan National Forest in north central Washington.

Site	Elevation (m)	Veg. Series	Parent Material	Species Studied
Umatilla N.F.				
313 Pomeroy #1	1675	ABLA	Basalt	GF/LP
314 Pomeroy #2	1525	ABGR	Basalt	DF/GF
315 Tollgate #1	1370	ABGR	Basalt	GF/PP
316 Tollgate #2	1675	ABGR	Basalt	GF/PP
317 Heppner #1	1455	ABGR	Basalt	DF/LP
318 Heppner #2	1465	ABGR	Basalt	PP
319 Heppner #3	1465	ABGR	Basalt	DF/PP
320 Ukiah	1465	ABGR	Basalt	PP
Okanogan N.F.				
327 Benson Creek	1025	PSME	Tonalite	PP
328 Blue Thin	1585	ABLA	Ash/Glacial Till	LP
329 Cooper Creek	1675	PSME	Granodiorite	LP/PP
330 Lost Thin	885	PSME	Ash/Glacial Till	PP
331 Black Pine	1585	ABLA	Glacial Till/Granite	LP
332 South Boulder	1510	ABLA	Glacial Till/Granite	LP
333 Bonaparte	1295	ABLA	Ash/Glacial Till	LP
334 Granite Creek	1235	PSME	Glac.Till/Lacustrine	LP

Design and Treatments

The Umatilla study was established in 1991, and the Okanogan study in 1993. Each study site, or installation, consists of six square plots 0.112 hectare in size, with a 6.1 to 12.2 meter buffer strip around each plot. For treatment, each installation was divided into two blocks of three plots based on tree and site similarities. Three treatments were then randomly assigned to the three plots in each block. For the Umatilla trials, the three treatments were: no fertilization, 224 kg/ha N, and 224 kg/ha N + 112 kg/ha S (N+S). For the Okanogan study, the three treatments were: unfertilized controls, 224 kg/ha N, and 224 kg/ha N+ 190.4 kg/ha K (N+K). On the N and N+K treatments, the N was applied as urea, and the K as red potash (KCl). On the N+S treatments, the S and part of the N were supplied by ammonium sulfate, and the remainder of N by urea. Fertilization was conducted in the fall of the establishment year.

Measurements and Laboratory Analysis

Foliage samples were collected during the dormant season at the end of the growing season one year after fertilization. The two most prevalent species on each installation were determined, and foliage samples were collected from two dominant trees for each species on each plot (see Table 1 for species per installation). This selection procedure resulted in two foliage samples per plot if one species was sampled, and four per plot if two species were sampled, resulting in totals of twelve and twenty-four foliage sample trees per installation, respectively. Foliage was collected from Douglas-fir, grand fir, lodgepole pine, and ponderosa pine trees, in various combinations depending on the installation. Current season foliage was collected from the top of each tree at the third whorl, placed in plastic bags, and stored in ice-cooled containers. In the laboratory, samples were oven-dried at 70 degrees centigrade for 24 hours, needles were separated from stems, and the separated needles were re-dried at 70 degrees centigrade for another 24 hours. For each sample tree, three repetitions of 50 needles were counted and weighed for calculation of needle weights, and foliage was then ground in preparation for chemical analysis.

Results of chemical analyses for N, K and S are reported in this paper since they were the nutrients applied in this study. Foliar N levels were determined using a standard micro-Kjeldahl procedure (Bremner and Mulvaney 1982). Needles were digested with sulfuric acid and the digestrate was distilled with steam. Total K was measured by atomic absorption spectroscopy. Total S was analyzed using a Leco sulfur analyzer.

Data Analyses

Foliar Nutrients

For each species studied, critical nutrient concentration levels reported in the literature are presented in Table 2. If foliar nutrient concentrations are below critical levels, trees are considered to be deficient in those nutrients. Also noted in Table 2 are the methods by which the critical nutrient levels were determined by the cited authors. Critical S levels for grand fir, lodgepole pine and ponderosa pine were determined using an optimal ratio method in conjunction with their critical N levels (Turner and Lambert 1987, Webster and Dobkowski 1983, Ingestad 1971). This method utilizes the known biochemical association between foliar N and foliar S to determine the minimum foliar S concentration considered necessary for N utilization. An N/S ratio of 14.7 is considered optimal for Douglas-fir and radiata pine (Blake et al. 1990, Turner and Lambert 1987, Kelly and Lambert 1972). We used the same ratio

(14.7) for grand fir, lodgepole pine and ponderosa pine. Additional research to experimentally determine critical S levels for these northwest conifer species is needed.

Table 2. Critical foliar nutrient concentrations for several conifer species that occur in mixed conifer stands in the inland northwest.

Foliar Nutrient Concentration	Douglas-fir[a]	True fir[b]	Lodgepole Pine[c]	Ponderosa Pine[d]
N (%)	1.40[1]	1.15[3]	1.20[1]	1.10[3]
P (%)	0.12[1]	0.15[3]	0.12[1]	0.08[3]
K (%)	0.60[1]	0.58[2]	0.50[1]	0.48[2]
S (%)	0.11[2]	0.08[4]	0.09[4]	0.08[4]
Ca (%)	0.15[1]	0.12[2]	0.08[1]	0.05[2]
Mg (%)	0.08[1]	0.06[2]	0.09[1]	0.05[2]

Values obtained by:
- [1] Best estimate by cited author based on literature review and personal experience
- [2] Derived by cited author using optimal proportions
- [3] Derived by cited author experimentally
- [4] Critical S values derived for this paper using an N:S ratio 14.7 in conjunction with the given critical N values (Blake et al. 1990, Turner and Lambert 1987)

[a] From Webster and Dobkowski (1983)
[b] All values except S from Powers (1983). S value calculated as noted above.
[c] All values except S from Ballard and Carter (1986), based on Everard (1973) and Swan (1972). S value calculated as noted above.
[d] Value for N from Powers et al. (1985), values for P, K, Ca and Mg from Powers (1983). S value calculated as noted above.

In addition to critical nutrient concentration levels, foliar nutrient ratios have often been used as a means of assessing nutrient status of forest trees. In this study, we examined foliar N/S and foliar K/N ratios in addition to foliar N, K and S levels. The N/S ratio was of particular interest because this ratio has been found to be a useful indicator of foliar S status of trees (Marschner 1986, Turner and Lambert 1987). The same foliar N/S ratio of 14.7 has been found for Douglas-fir and radiata pine (Turner and Lambert 1987, Kelly and Lambert

1972). A foliar N/S ratio below 14.7 suggests that sufficient S is present for proper N utilization. A foliar N/S ratio above this level means that N is excessive relative to foliar S concentration, and may indicate an induced sulfur deficiency, particularly if foliar N levels are below critical. In addition to N/S ratios, foliar K/N ratios were also calculated as a measure of nutrient balance. Excess N in relation to K is thought to make forest trees more susceptible to insects and diseases (Moore et al. 1994). Ingestad (1967, 1979) suggested that for all conifers a foliar K/N ratio of 50% is critical, while a ratio of 65% is optimal.

For each of the four species studied, the following foliar nutrient variables were examined: foliar concentration (%) and content (needle weight x % concentration) for N, K, and S, as well as N/S and K/N ratios. The foliar values for each variable were averaged for the two trees sampled for each species on each plot. The mean values were graphically analyzed using an empirical cumulative distribution: the vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Differences between the distributions for the various fertilizer treatments were tested for significance using the Kolmogorov-Smirnov criterion, and were considered significant at $p=.10$ (Lehman 1975, Kim and Jennrich 1973). The critical foliar nutrient concentrations or ratios are represented by a vertical line at the appropriate level for each species, as shown in Table 2.

Volume Growth Response

We analyzed four-year volume growth response of the dominant species on each site. Tree measurements for height and diameter were made at the time of plot setup, and at the end of the fourth growing season following fertilization. Volumes were calculated using speciesspecific volume equations developed for trees in the inland northwest region (Wykoff et al. 1982). Gross volumes at year 0 and year 4 for were summed for each plot for the same dominant species examined during foliar analyses (see Table 1 for species per installation). For each species and plot, gross volume growth for the four-year period following fertilization was calculated as follows:

$$RVG_4\,(\%) = \frac{(GV_4 - GV_0)}{GV_0} * 100 \qquad (1)$$

Where:
RVG = Gross volume growth at year 4 relative to initial volume (year 0)
GV = Gross volume at fertilization (year 0) and at year 4 after fertilization

To minimize scaling problems due to differences in tree size, and thus better assess the effects of fertilization on tree growth, we calculated volume response of each fertilized plot relative to the control plot as in equation (1). The six plots for each installation were grouped into the two blocks of three assigned during installation establishment, and control plot relative growth was used as a scale factor for the two treated plots within each block to determine relative volume response of the treated plots as follows:

$$RVR_T\,(\%) = \frac{(RVG_T - RVG_C)}{RVG_C} * 100 \qquad (2)$$

Where:
RVR = Volume response of the treated plots relative to control plot growth
RVG = Relative volume growth of the treated (T) and control (C) plots calculated using Equation 1 above.

The relative volume response values for the fertilized plots were grouped by treatment, and their distributions graphically analyzed in the same way as foliar nutrient data, with volume response depicted on the horizontal axis of the cumulative distribution graph. Since control plot relative growth was used as the scale factor, control response was depicted by a vertical line at the zero response level on the horizontal axis. The Kolmogorov-Smirnov criterion was again used to test for differences between distributions for various treatments ($p=.10$), and a Student's *t*-test was also performed to determine whether the mean of each treatment distribution differed from the control response of 0.

Results

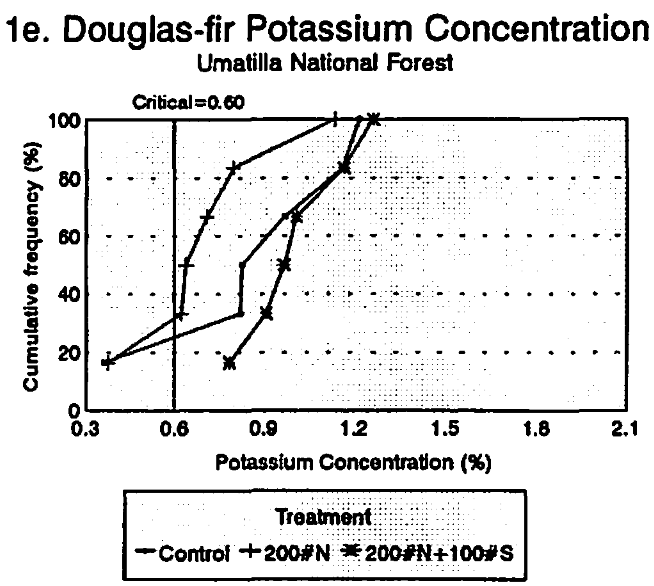
Douglas-fir

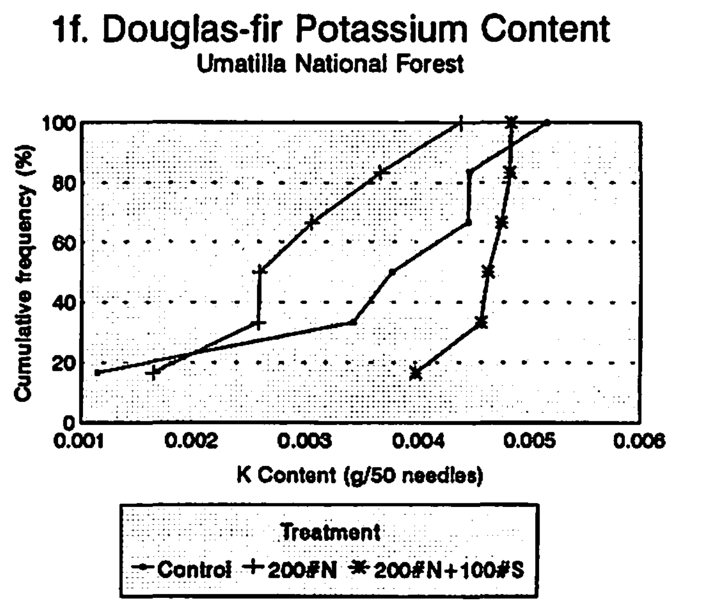
Foliar nitrogen and sulfur response

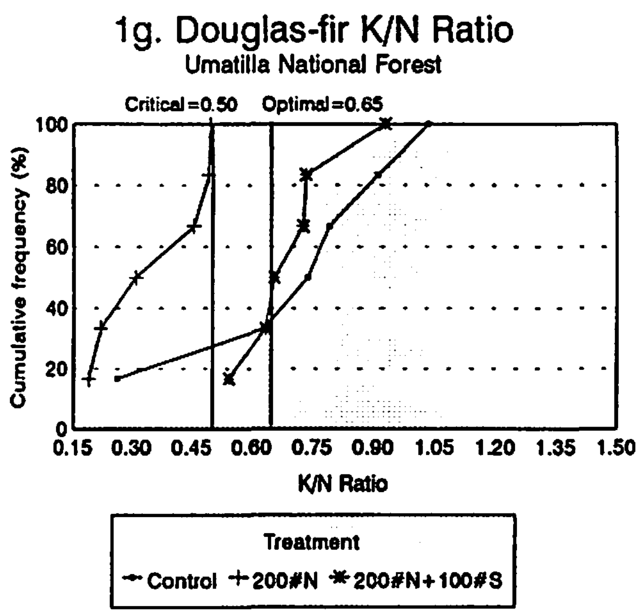
The relative cumulative frequencies of foliar N concentrations of Douglas-fir on the Umatilla N.F. are shown by treatment in Figure 1a. Without fertilization, all of the plots tested were deficient in N. All plots that were fertilized with N showed increased N concentrations, with the magnitude of response depending on treatment. The greatest response in foliar N levels occurred when N was applied as urea, with 100% of the plots showing N concentrations above the critical threshold after fertilization. When N was applied in combination with S, however, foliar N concentrations were significantly lower than those for N alone, with only about 50% of the plots having N concentrations above critical values. Distributions for both fertilizer treatments were significantly greater than the control distribution, and the N and N+S treatments were also significantly different from each other.

The distribution of total foliar S concentrations for Douglas-fir on the Umatilla N.F. are provided in Figure 1b. All of the control plots and the N-alone plots had below-critical S levels, with no apparent difference in S uptake by treatment. The plots receiving N+S did

Figure 1e-1f: Relative frequency distributions of foliar K concentrations, K contents, K/N ratios, and four year volume response for Douglas-fir following fertilization with N and N+S on the Umatilla National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. Relative volume responses are illustrated in a similar fashion, with control levels set to zero and indicated by a vertical line.







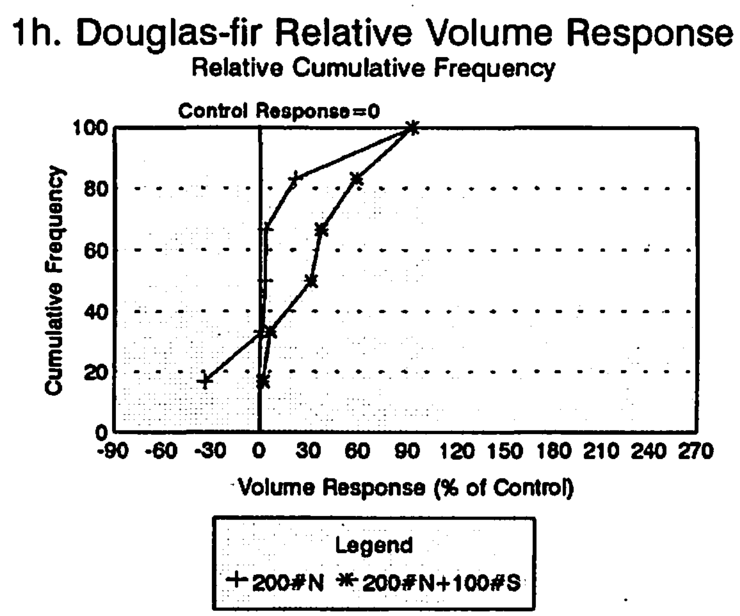
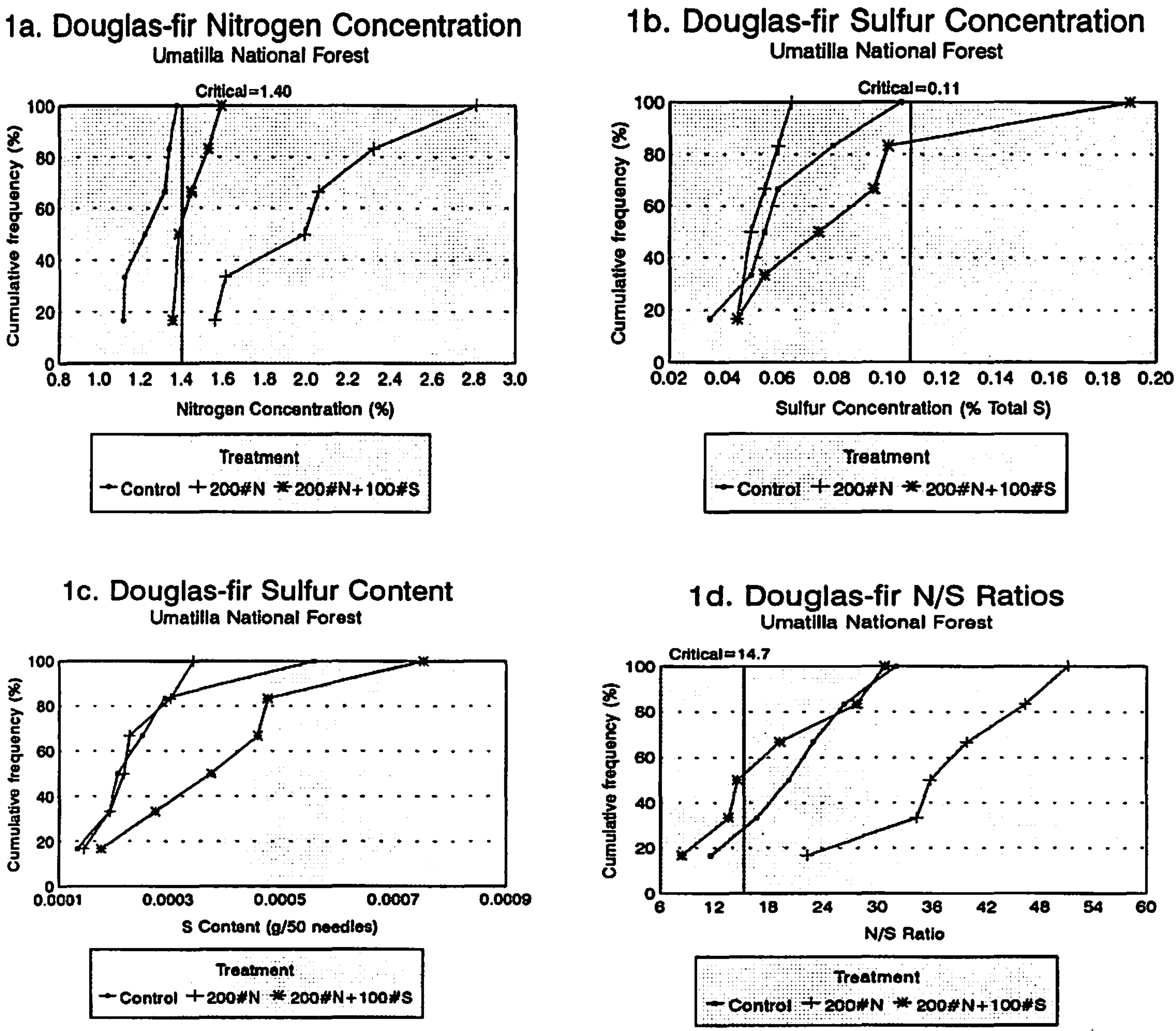


Figure 1a-1d: Relative frequency distributions of foliar N and S concentrations, S contents and N/S ratios for Douglas-fir following fertilization with N and N+S on the Umatilla National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level.



show somewhat higher S concentrations than the control and N-alone treatments, however only one plot had above-critical S levels. Foliar S content parallels the results for Douglas-fir S concentration (Figure 1c). The distributions portrayed in Figures 1b and 1c did not differ significantly from each other; however, the trends indicate that some S uptake did occur on the N+S treatments.

Seventy five percent of the Umatilla Douglas-fir control plots had excessive foliar N/S ratios (Figure 1d). Following fertilization with N alone, 100% of the plots showed excessive N/S ratios. Following N+S fertilization, the N/S ratios were excessive on only 50% of the test plots, and did not differ significantly from control levels (Figure 1d).

Foliar potassium response and potassium/ nitrogen ratios

The relative cumulative frequency distribution for foliar K concentrations of Douglas-fir on the Umatilla is shown in Figure 1e. Control levels indicate that K levels were above critical on about 75% of the sites prior to fertilization. Following fertilization with N alone, K levels were still above critical 70% of the time, but tended to be lower than control levels. When N+S fertilizer was applied, all of the plots showed K concentrations above critical, and the K levels were significantly higher than on the N-alone plots. Foliar K contents were also examined by treatment (Figure 1f). The plots receiving N alone had lower K contents than the control plots about 70% of the time. The plots receiving N+S had higher K content than all but one control plot, and significantly more K than the N-alone plots 100% of the time. In other words, the Douglas-fir on the Umatilla showed decreased K uptake following N fertilization, and increased K uptake following N+S fertilization, and foliar K content analysis indicated that this was not a growth dilution effect.

As noted previously, 50% and 65% respectively are considered critical and optimum K/N ratios for most conifer species. The .50 and .65 levels are both depicted in Figure 1g along with foliar K/N ratio distributions for the Umatilla N.F. Douglas-fir. Foliar K/N ratios on the control plots were below critical 30% of the time, and above optimal about 60% of the time. Following N-only fertilization, K/N ratios decreased to sub-critical levels on all plots. Following N+S fertilization, foliar K/N ratios were above critical on all plots, and above optimal about 50% of the time. Overall, the K/N ratio was best maintained when S was applied along with N fertilization. The N+S treatment resulted in above-critical K/N ratios on all plots, whereas 30% of the control plots and all of the N-alone plots had below-critical K/N ratios.

Growth response of fertilized Douglas-fir

The four-year volume growth response of Douglas-fir on the N-treated plots was greater than the control plot growth, which was adjusted to zero, about 70% of the time (Figure 1h). Volume response on the N+S plots was greater than control plot growth all of the time and on average, this response was statistically significant. The two fertilizer treatments were not significantly different from each other, though the N+S plots tended to show greater volume responses than the N-alone plots. Volume growth for Douglas-fir increased in response to both N and N+S during the four years following fertilization, and the N+S treatment gave the best growth response compared to the control plots.

Grand fir

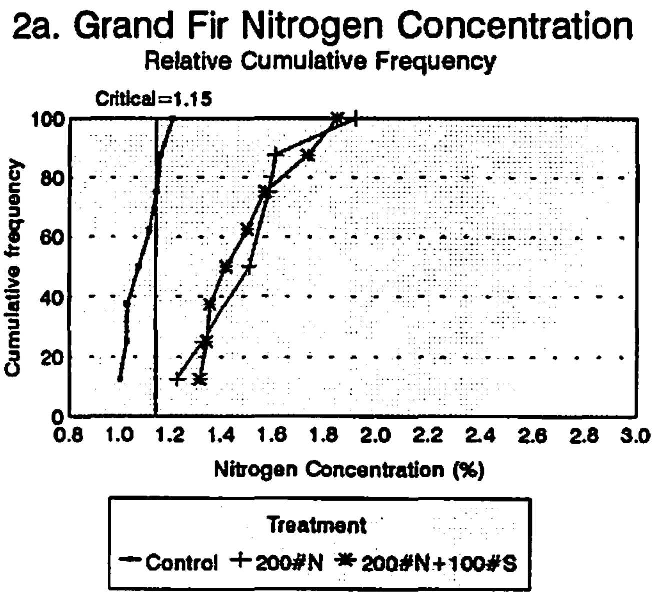
Foliar nitrogen, sulfur and potassium concentrations

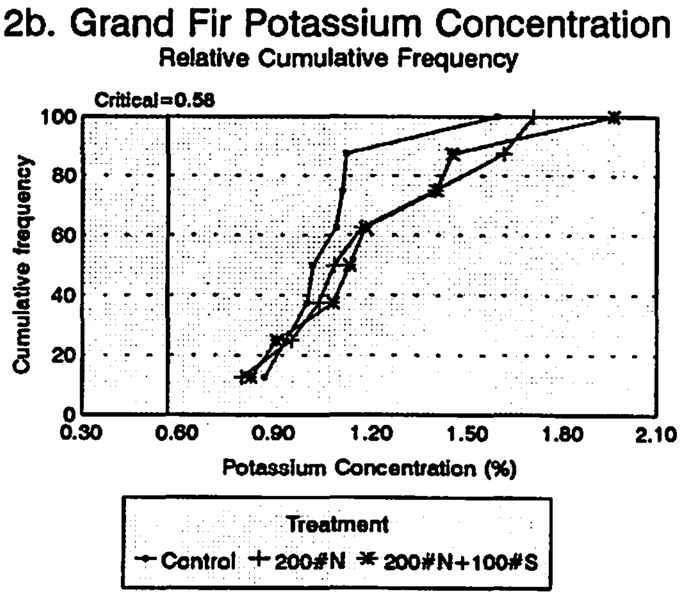
Grand fir was analyzed on four sites on the Umatilla National Forest. Cumulative distributions of grand fir foliar N concentrations by treatment are shown in Figure 2a. Approximately 75% of the control plots had foliar N concentrations below critical levels. Following application of both N and N+S, all plots showed above-critical N levels. The differences between control and both fertilizer treatments were significant, though there was no significant difference between the two treatments. Grand fir took up the applied N, and the application of S along with N did not significantly affect foliar N concentration after treatment.

Grand fir foliar potassium concentrations were above critical on all plots, both with and without fertilization (Figure 2b). Foliar K concentrations tended to be higher on fertilized than control plots for both N and N+S treatments, with K concentrations exceeding those of the control plots about 70% of the time. Fertilization somewhat enhanced the ability of grand fir to take up K. There was no significant difference in foliar K concentration between the N and N+S treatments, indicating that the application of S in addition to N did not affect the K uptake capacity of grand fir.

Grand fir foliar K/N distributions are shown by treatment in Figure 2c. The critical K/N ratio of 0.50 and the adequate ratio of 0.65 are plotted in a similar manner as for Douglas-fir. Due to the relatively high foliar K concentrations of grand fir, K/N ratios remained above the critical value for essentially all of the plots regardless of treatment. Foliar K/N ratios were above adequate (0.65) about 80% and 70% of the time respectively for the N and N+S treatments.

Figure 2a-2c. Relative frequency distributions of foliar N and K concentrations and K/N ratios for grand fir following fertilization with N and N+S on the Umatilla National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level.





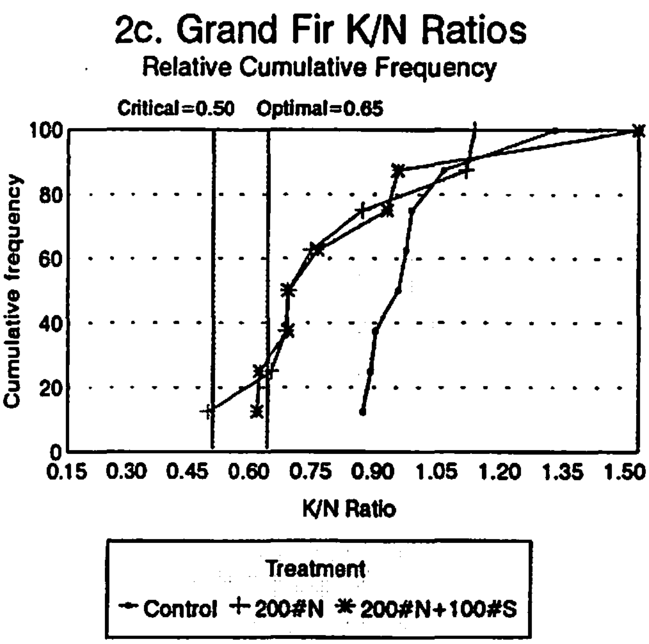
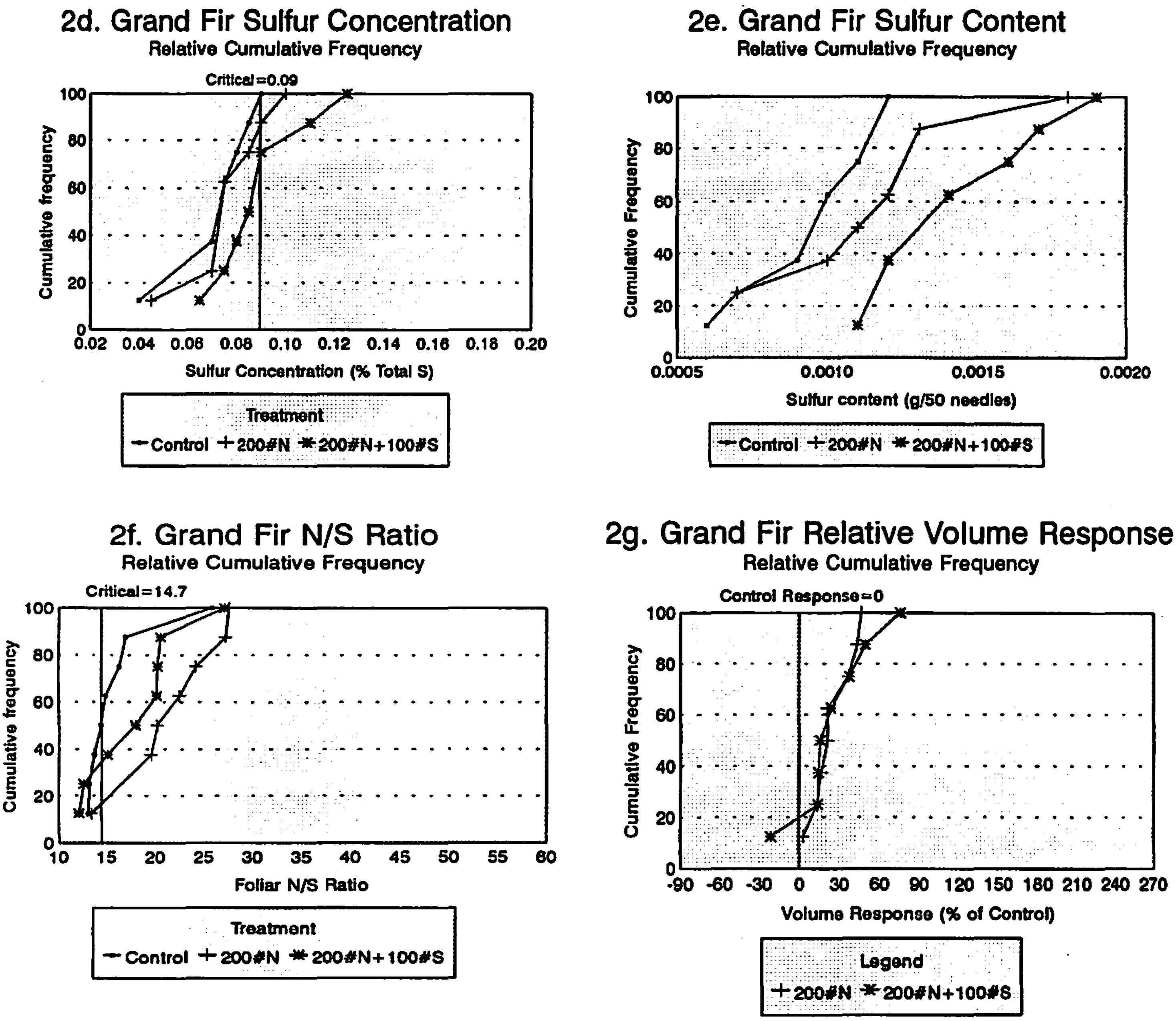


Figure 2d-2g. Relative frequency distributions of foliar S concentration and Content, foliar N/S ratios and four year volume response for grand fir following fertilization with N and N+S on the Umatilla National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. Relative volume responses are illustrated in a similar fashion, with control levels set to zero and indicated by a vertical line.



Foliar S concentrations for grand fir were below critical levels on all of the control plots (Figure 2d). About 90% of the plots receiving the N-only treatment showed S concentrations below critical one year after fertilization, while 75% of the plots receiving the N+S treatment were below the critical level. The N-only foliar S concentrations were not significantly different from the control plots. The N+S plots, however, showed higher S concentrations than the N-alone and control plots, suggesting that S uptake occurred when S was applied with N. Analysis of foliar S contents for grand fir (Figure 2e) showed that plots receiving N+S fertilization had significantly greater foliar S contents than the control plots, confirming S uptake. This result was also apparent from the N/S ratios (Figure 2f), showing that the N/S ratios were generally better (lower) on the N+S plots than the N-alone plots, though at optimal levels only about 30% of the time.

Growth response of fertilized grand fir

Grand fir growing on both the N and N+S plots showed significantly greater four-year relative volume growth responses than the control plots (figure 2g). There was no significant difference between volume response on the N and N+S plots, indicating that the addition of S did not affect the growth response to N fertilization.

Lodgepole Pine

Analysis of variance showed that lodgepole pine nutrient concentrations and responses did not differ between the Umatilla and Okanogan National Forests, allowing us to combine these data. Therefore, four treatments are presented on each cumulative distribution graph, representing the control and the N-alone treatment for both Forests combined, and the N+S and N+K treatments for the Umatilla and Okanogan Forests respectively.

Foliar nitrogen and potassium concentrations and K/N ratios

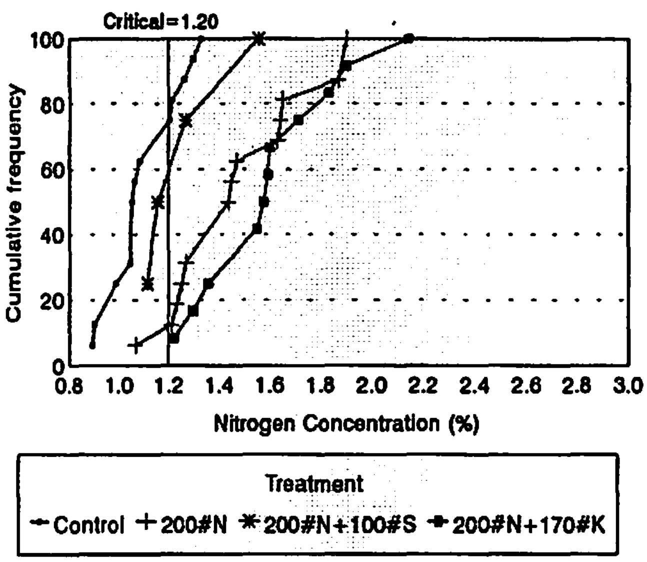
The relative cumulative frequency diagram for lodgepole pine foliar N concentrations is provided in Figure 3a. Nitrogen was deficient on 70% of the unfertilized plots. Foliar N concentrations increased significantly over that of the controls on all plots fertilized with N, regardless of whether K or S was also applied (Figure 3a). One year after treatment, foliar N concentrations were above the critical level on 40% of the plots fertilized with N+S, on 90% of the plots receiving N-alone, and on 100% of the plots receiving N+K fertilization. Foliar N concentrations were lower on the N+S plots than on the N or N+K treated plots.

Lodgepole pine control plots had foliar K concentrations below critical levels about 25% of the time (Figure 3b). Following the application of N alone, 35% of the plots had K concentrations below critical levels. When N+S was applied, 50% of the plots were below-critical K levels. One year following N+K fertilization, none of the plots showed deficient foliar K concentrations. To better demonstrate changes in K uptake following treatment, foliar K contents for the Okanogan plots are also provided (Figure 3c). Lodgepole pine foliar K content was significantly higher on the N and N+K treated plots than on the control plots. Lodgepole pine control plots showed the best foliar K/N ratios, with 70% of the plots above critical and 15% of the plots above optimal levels (Figure 3d). One year following fertilization with N alone, 90% of the plots had K/N ratios below critical level, and all were below optimal. Following N+S fertilization, 80% of the plots showed sub-critical K/N ratios, and 95% of the plots were below the optimal ratio. All plots were below the critical ratio one year after N+K fertilization. The general trend of lower K/N ratios one year after fertilization was due to a combination of increased N uptake and decreased K uptake on the plots receiving N fertilization.

Figure 3a-3d. Relative frequency distributions of foliar N and K concentrations, K contents and K/N ratios for lodgepole pine following fertilization with N and N+S on the Umatilla National Forest, and N and N+K fertilization on the Okanogan National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level.

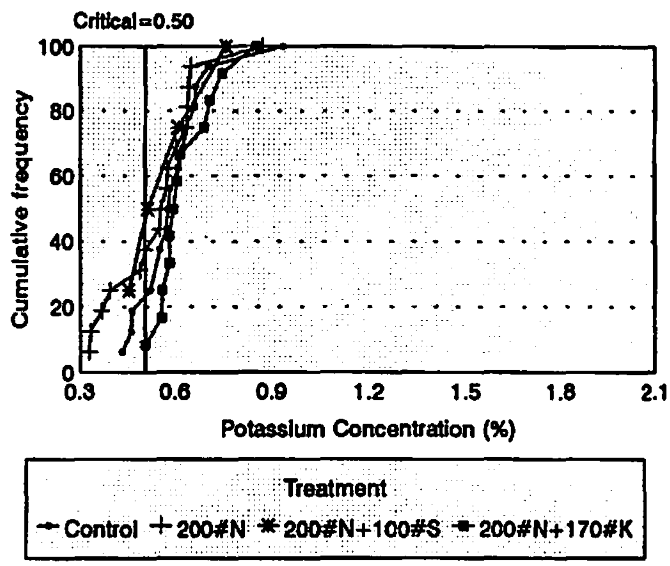
3a. Lodgepole Pine Nitrogen Concentration

Relative Cumulative Frequency



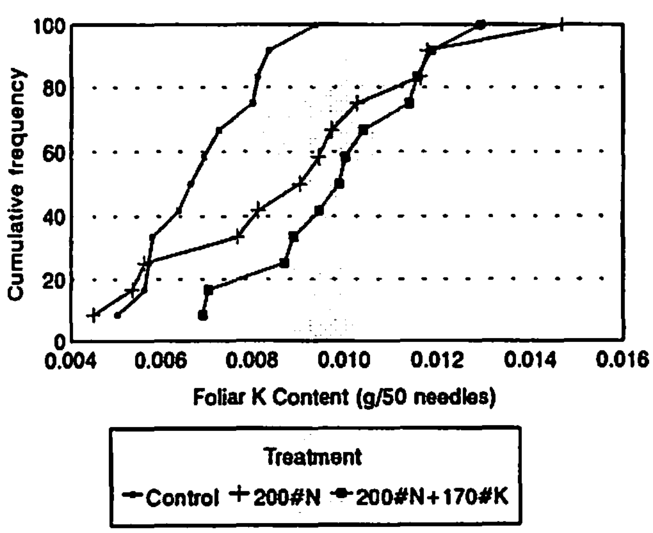
3b. Lodgepole Pine Potassium Concentration

Relative Cumulative Frequency



3c. Lodgepole Pine Potassium Content

Okanogan National Forest



3d. Lodgepole Pine K/N Ratio

Relative Cumulative Frequency

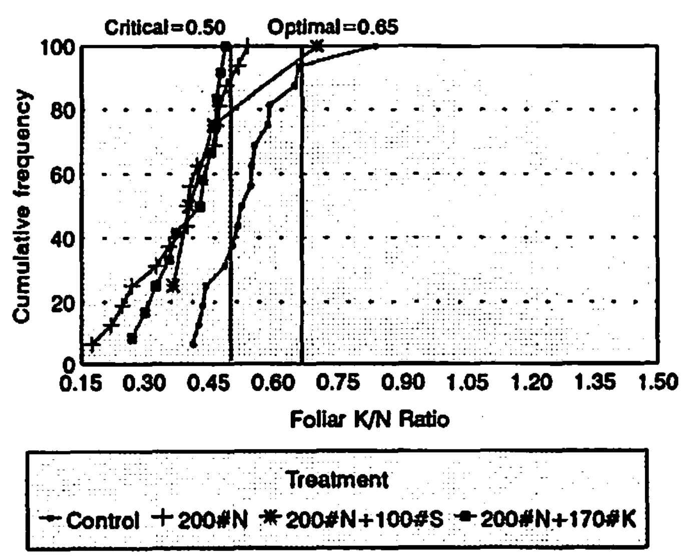
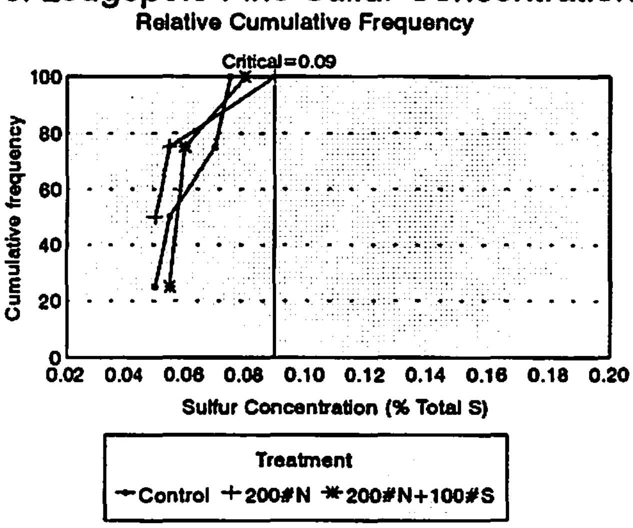
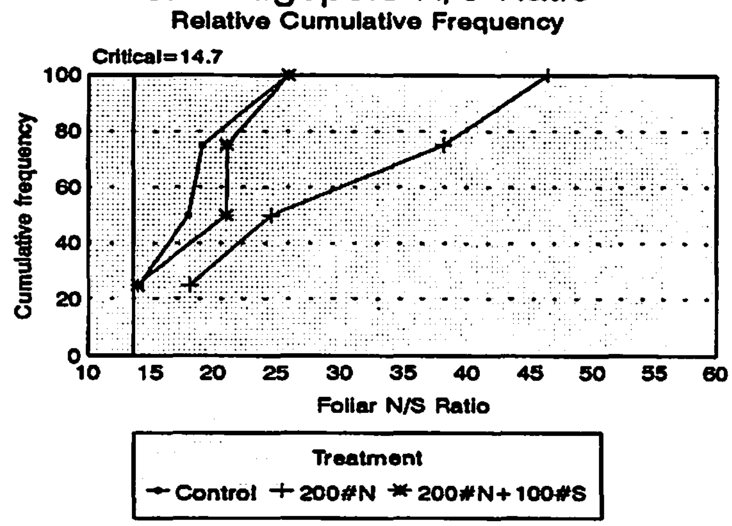


Figure 3e-3g. Relative frequency distributions of foliar S concentration, foliar N/S ratios and four year volume response for lodgepole pine following fertilization with N and N+S on the Umatilla National Forest, and N and N+K fertilization on the Okanogan National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. Relative volume responses are illustrated in a similar fashion, with control levels set to zero and indicated by a vertical line.

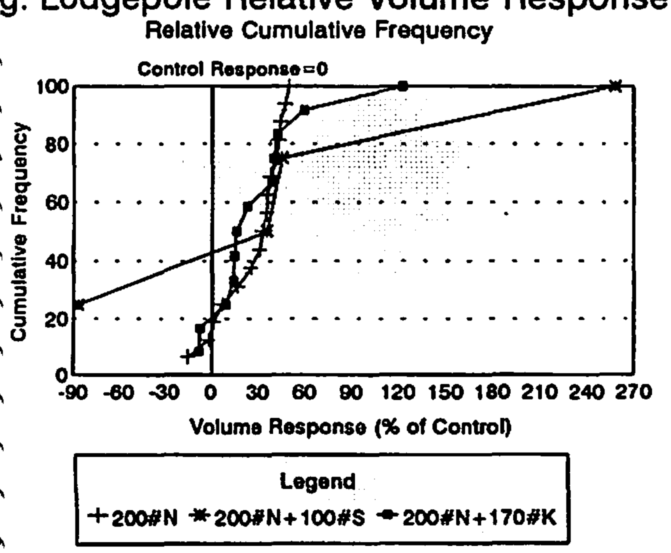
3e. Lodgepole Pine Sulfur Concentration



3f. Lodgepole N/S Ratio



3g. Lodgepole Relative Volume Response



Foliar sulfur concentrations and N/S ratios

Foliar S concentrations were below critical for lodgepole pine on all control and fertilized plots (Figure 3e). There were no significant differences between S concentrations for the different treatments, and this was confirmed by S content analysis that showed no significant treatment effects. This indicates that S uptake did not occur, even on the plots that received the N+S treatment.

The cumulative distributions of foliar N/S ratios for lodgepole pine by treatment are plotted in Figure 3f along with the presumed optimal ratio of 14.7. All Umatilla N.F. lodgepole pine study plots had excessive N/S ratios, regardless of whether or not they received fertilization. Although the control plots had the best (lowest) N/S ratios compared to treated plots, they also tended to be N-deficient, indicating a probable nutrient imbalance on those plots. The plots receiving the N alone treatment had the worst (largest) N/S ratios, however since the foliar N concentrations were above critical levels for most of these plots, the high ratio is not of great concern. The plots receiving N+S showed a better N/S balance than the plots receiving N alone, but since N was deficient 60% of the time on those plots, nutrient imbalance may be a problem.

Growth response of fertilized lodgepole pine

The relative volume response for lodgepole pine is shown in Figure 3g. Responses for both the N-alone and N+K fertilization were significantly greater than the control response (zero), though they were not significantly different from each other. Lodgepole pine showed strong volume response to N fertilization, and that the addition of K along with N did not affect the response significantly. The N+S fertilization treatment, however, produced extremely variable volume growth response. Overall, the N+S volume response did not differ from the control response of zero, nor did it differ significantly from the N and N+K treatments. The N+S response did, however, show both the most negative response (-90% of control growth) and the highest positive response (+250% of control growth) shown by lodgepole pine in this study.

Ponderosa Pine

Ponderosa pine occurred on five installations on the Umatilla N. F., and on three sites on the Okanogan N.F. As with lodgepole pine, analysis of variance for ponderosa pine showed that nutrient concentrations and responses did not differ between the National Forests, allowing us to combine these data. The four treatments are again presented on each graph, with the control and the N-alone treatments for both regions combined, and the N+S and N+K treatments for the Umatilla and Okanogan Forests respectively.

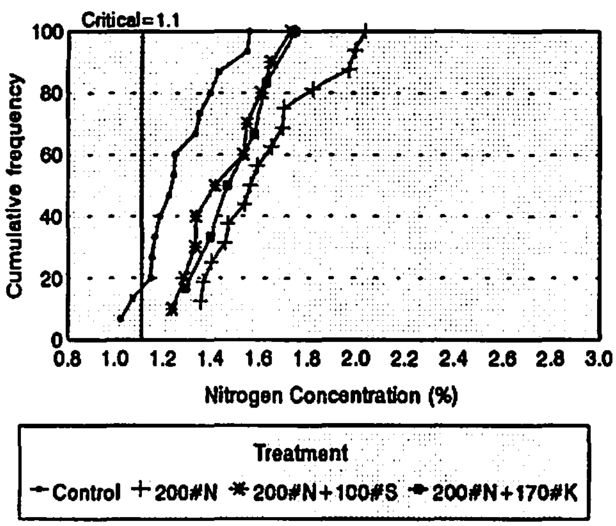
Foliar nitrogen and potassium concentrations and K/N ratios

Foliar N concentrations for ponderosa pine growing in unfertilized mixed conifer stands were above critical levels about 85% of the time (Figure 4a). One year after fertilization, all of the fertilized plots had foliar N concentrations significantly greater than control levels, indicating that N uptake did occur during the first growing season after treatment. The plots receiving N-alone had the highest foliar N concentrations, followed by the N+K and N+S plots, respectively. Compared to published critical levels (Table 2), N was not deficient for ponderosa pine in mixed conifer stands. However, the trees actively took up applied fertilizer N, and this was reflected in foliar N contents as well (graph not shown).

Figure 4a-4d. Relative frequency distributions of foliar N and K concentrations, foliar K contents and foliar K/N ratios for ponderosa pine following fertilization with N and N+S on the Umatilla National Forest, and N and N+K fertilization on the Okanogan National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level.

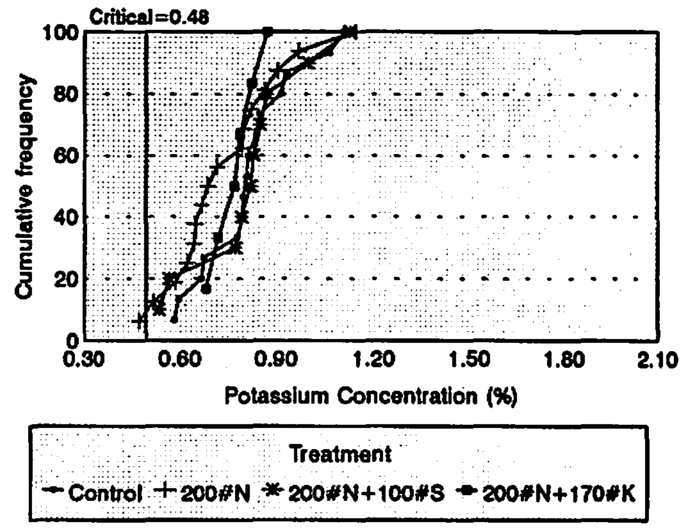
4a. Ponderosa Pine Nitrogen Concentration

Relative Cumulative Frequency



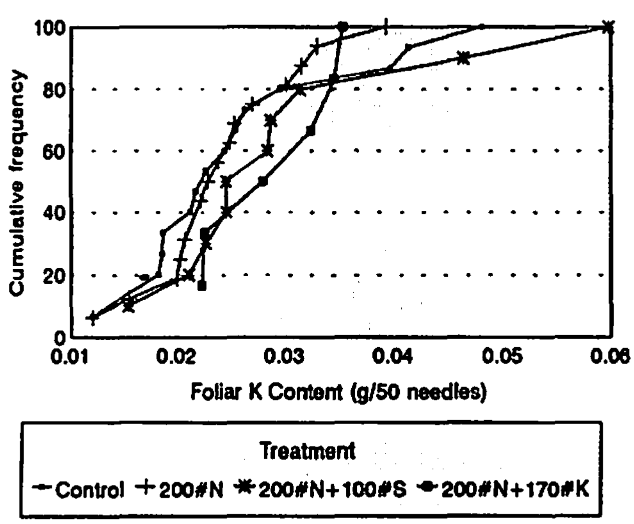
4b. Ponderosa Pine Potassium Concentration

Relative Cumulative Frequency



4c. Ponderosa Pine Potassium Content

Relative Cumulative Frequency



4d. Ponderosa Pine K/N Ratio

Relative Cumulative Frequency

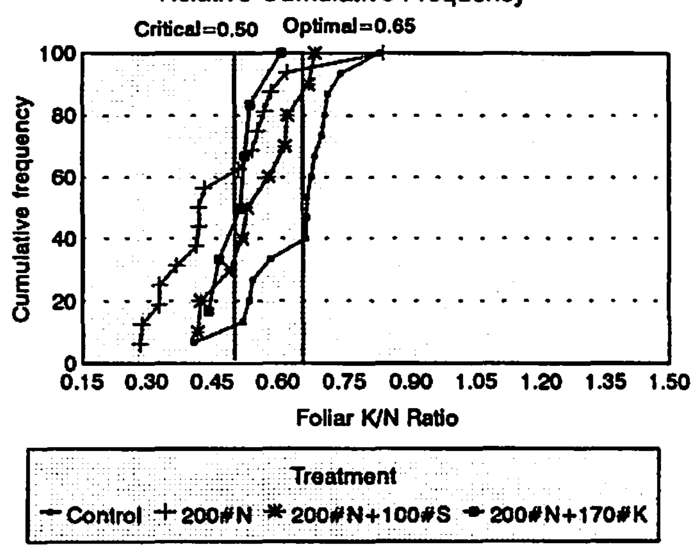
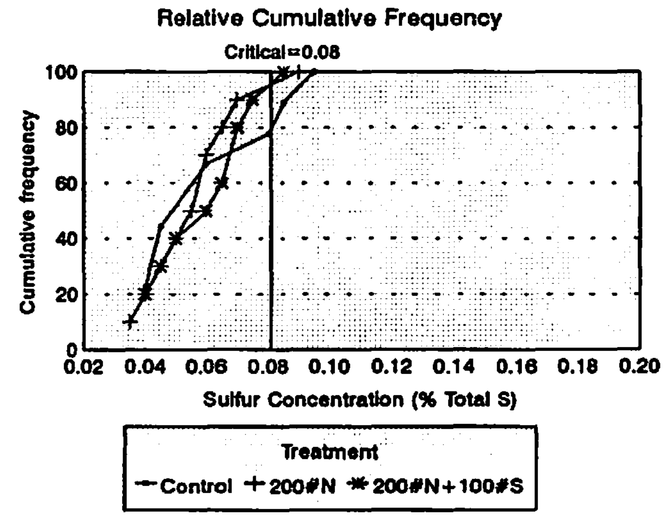
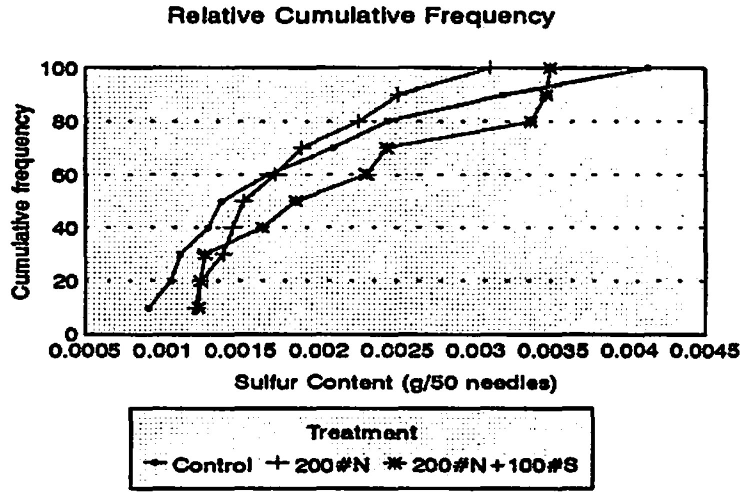


Figure 4e-4h. Relative frequency distributions of foliar S concentrations and contents, foliar N/S ratios and four year volume response for ponderosa pine following fertilization with N and N+S on the Umatilla National Forest, and N and N+K fertilization on the Okanogan National Forest. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content or ratio given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. Relative volume responses are illustrated in a similar fashion, with control levels set to zero and indicated by a vertical line.

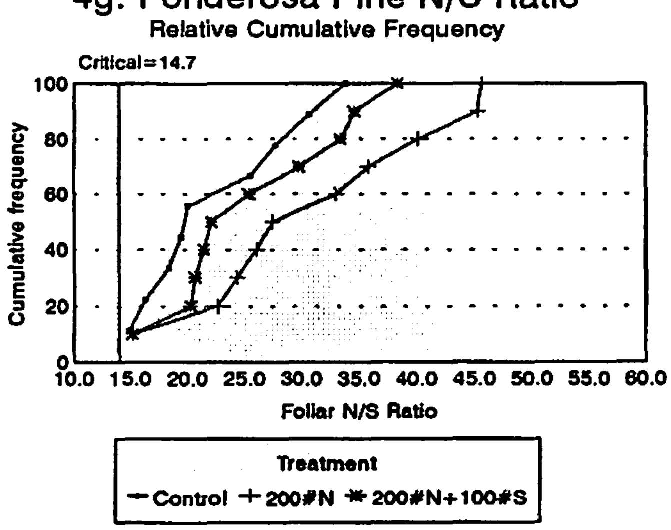
4e. Ponderosa Pine Sulfur Concentration



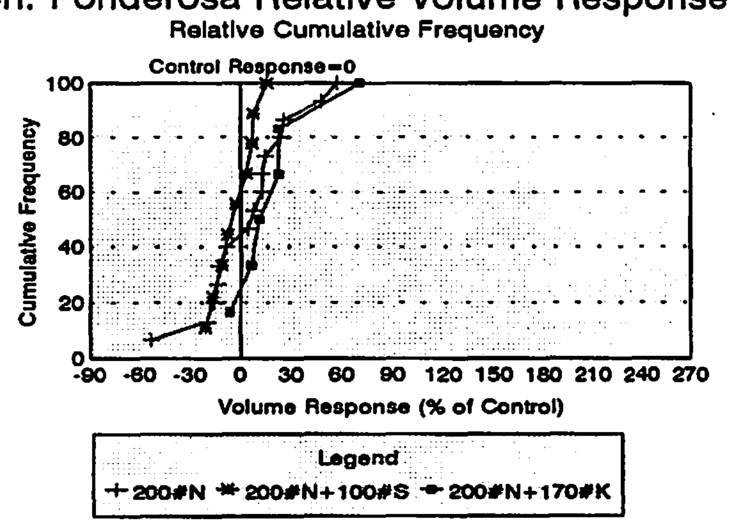
4f. Ponderosa Pine Sulfur Content



4g. Ponderosa Pine N/S Ratio



4h. Ponderosa Relative Volume Response



Ponderosa pine foliar K concentrations were also above critical levels on unfertilized plots. However, one year after fertilization there were no significant differences between the control plots and any of the treatments for either K concentration or content (Figures 4b and 4c). Ponderosa pine in mixed conifer stands did not seem to take up applied fertilizer K, and the addition of N with or without K did not affect K uptake rates. Potassium concentrations after fertilization were about the same for the N+K and N+S treatments, and generally tended to be lower than K concentrations on the control and N-alone plots.

Foliar K/N ratios for ponderosa pine were above critical (0.5) on 90% of the control plots, and above optimal (0.65) on 60% of the control plots (Figure 4d). Following fertilization with N alone, foliar K/N ratios were below critical on 60% of the plots, and below optimal 90% of the time. Following N+S fertilization, about 30% of the plots were below critical levels, and 90% were below the optimal ratio. Foliar K/N ratios on the N+K plots were below critical about 45% of the time, and below optimal on all of the plots. The foliar K/N ratios for ponderosa pine were highest on the control plots, which primarily reflected the low N concentrations on those plots relative to the fertilized plots. Foliar K/N ratios were the next highest on the N+S plots, due to increased K uptake and decreased N uptake on those plots relative to the other fertilized plots. The next highest foliar K/N ratios for ponderosa pine were on plots fertilized with N+K, reflecting the tendency towards decreased foliar K concentrations compared to N+S and control plots. Foliar K/N ratios were lowest on plots fertilized with N-alone, a result of the high foliar N concentrations on those plots.

Foliar sulfur concentrations and N/S ratios

Foliar S concentrations for ponderosa pine were deficient on 80% of the control plots, and on 95% of the plots receiving N and N+S fertilization (Figure 4e). Overall, the N and N+S treatments had no significant effect on foliar S concentrations after one growing season. However, foliar S contents (Figure 4f) did increase on the N+S plots, providing evidence for S uptake by ponderosa pine, and also indicating growth dilution of S concentration induced by N fertilization.

Foliar N/S ratios for ponderosa pine in mixed conifer stands were always excessive (>14.7), regardless of whether the stand was fertilized (Figure 4g). Since foliar N concentrations for ponderosa pine were above critical levels on all of the fertilized plots and on 85% of the unfertilized plots (Figure 4a), the high N/S ratio does not necessarily indicate an imbalance. However, there may be an N/S imbalance on the 15% of the control plots where N was deficient. The N+S treatment kept the N/S ratio closer to the acceptable critical level of 14.7, compared to application of N alone.

Growth response of fertilized ponderosa pine

Relative volume growth response of ponderosa pine four years after any fertilizer treatment was non-significant (Figure 4h). Furthermore, none of the volume responses for the different treatments differed significantly from each other. The N+K treatment did produce marginally significant response ($p=.1077$). Overall, however, the results show that when growing in mixed conifer stands, ponderosa pine did not respond strongly to fertilization during the first four years after treatment.

Discussion

Without fertilization, all Douglas-fir sample plots showed inadequate foliar N concentrations. Most unfertilized grand fir and lodgepole pine plots also showed inadequate foliar N, while most ponderosa pine foliage samples were above critical N levels. This seems to indicate that ponderosa pine in mixed conifer stands were able to obtain adequate N, while the other three conifers were unable to do so. After fertilization with N-only, Douglas-fir, grand fir and ponderosa pine had adequate foliar N on all plots, while lodgepole pine had adequate foliar N on 90% of the fertilized plots. Nitrogen uptake was uniformly good for all species after treatment with urea at a rate of 224 kg N per hectare. However, foliar N concentrations did not increase as consistently following the N+S treatments as for N-only, even though the elemental N rate was the same. Although all four species showed significant foliar N increases following N+S fertilization, only 50% of the Douglas-fir and 40% of the lodgepole pine plots were above adequate. All grand fir and ponderosa pine plots were above critical foliar N levels following the N+S treatment. Nitrogen content analysis also confirmed that the N+S treatment was not as effective as N-only in increasing foliar N for Douglas-fir and lodgepole pine. The difference in foliar N concentrations by treatment may be a fertilizer effect, since the N+S supplied a portion of the N in ammonium sulfate form, while the other two treatments supplied 100% of the N as urea. Brockley (1995) found that while different fertilizer N sources resulted in different 1st year foliar N concentrations for lodgepole pine, the growth of the same trees was not affected by the different N source.

Except for two ponderosa pine plots, all species on all unfertilized plots showed inadequate foliar S concentrations. Following fertilization with either N or N+S, foliar S concentrations were not significantly different from control levels for any of the four species, although the grand fir and Douglas-fir showed tendencies toward increased S concentrations on the N+S plots. Analysis of foliar S contents confirmed that S uptake did occur on the N+S plots for grand fir, Douglas-fir and ponderosa pine, and this increase was significant for grand fir. This indicated that the lack of foliar S concentration response for these species was a growth dilution effect. The lodgepole pine did not show any changes in foliar S content or concentration following fertilization.

While foliar S concentration levels alone may be used to indicate potential nutrient deficiencies, the nutrient balance is also an important aspect of tree nutrition, as reflected in the foliar N/S concentration ratio. High N/S ratios may indicate an inability of the trees to properly utilize accumulated N supply for growth. In the presence of high N availability, S-deficient plants often accumulate certain amino acids which are high in N but do not contain S. This is a common method of storing excess N in S-limiting situations (Turner and Lambert 1987, Turner et al. 1977 and 1979, Turner 1979). Turner and Lambert (1987) found that for radiata pine, S deficiency was induced by N fertilization. They also found that in S-limited stands, the addition of N fertilizer could further induce S deficiency, and that the foliar S level prior to fertilization was useful for predicting growth response. High N/S ratios may not be a problem when N concentrations are above critical levels, but may indicate a potential inability to utilize stored N.

In our study, none of the unfertilized lodgepole or ponderosa pine samples showed adequate N/S ratios, and only 50% of the grand fir and 30% of the Douglas-fir plots had adequate N/S ratios. These results suggest that our sites may be extremely low in sulfur, and that S should be included along with N in the fertilizer blend. Poor N utilization was supported in our study by the fact that after fertilizing with N alone, foliar N/S ratios were inadequate for all lodgepole and ponderosa pine plots and for most grand fir and Douglas-fir plots. Furthermore, the increases in N/S ratios following N-only fertilization were significant for all species. In contrast, foliar N/S ratios following N+S fertilization did not differ significantly from the control plots for any of the four species. This indicated that the addition of S to the fertilizer blend prevented the significant increase in the foliar N/S ratio observed after fertilizing with N alone, and that the overall N/S ratio was better maintained through application of N+S versus N alone. Perhaps higher S fertilizer rates would have produced desirable decreases in the N/S ratio. Blake et al. (1990) found that foliar S levels did not increase significantly following N+S fertilization, however the 3 to 4 year growth response tended to be greater on N+S plots they studied than N alone. The low foliar S response in their study was attributed to either growth dilution effects or decreased S uptake on the N+S sites. In our study, foliar S contents of Douglas-fir, grand fir and ponderosa pine increased on N+S plots, indicating that some growth dilution did occur. Our results also suggest that S uptake was greater on the N+S treated plots than the N-alone or untreated plots.

All unfertilized grand fir and ponderosa pine plots showed foliar K concentrations above adequate levels. Over 75%of the Douglas-fir and lodgepole pine control plots had adequate K concentrations as well. The fertilizer treatments (N, N+S, N+K) had no significant effect on K concentration for any of the species sampled, indicating that K was adequate on our study sites. Foliar K contents did tend to increase following application of N+S for Douglas-fir and grand fir, and N+K for lodgepole pine. Foliar K contents increased significantly for the N+S treatment over N-alone for Douglas-fir, and for N+S over the control plots for grand fir. This K response of Douglas-fir and grand fir to N+S fertilization may be explained in part by the chemical properties of ammonium sulfate, particularly when applied to soils high in clay such as those derived from the basalts on our study areas. The ammonium ions in this fertilizer can compete with K^+ ions for sites on the soil exchange complex, resulting in an increase in exchangeable K available for plant uptake. This may also explain the lower foliar N response of those plots, as those ammonium ions are held on the soil exchange sites. While the same behavior may be expected of urea over time, the response is more immediate following ammonium sulfate application due to the immediate availability of a large concentration of ammonium.

The balance of foliar K and N (K/N ratio) is also important (Mika and Moore 1991). Plots without any fertilization treatments generally showed adequate balance over 60% of the time. After fertilizing with N-only, all species showed a significant decline in foliar K/N ratios, with all Douglas-fir and 90% of the lodgepole pine plots having inadequate K/N ratios. Generally, the N+S and N+K treatments also produced declines in the foliar K/N ratios for all species, although the decrease was often less than the N-only treatment. In our study, changes in foliar K/N ratios for all species were driven by foliar N concentration increases resulting from any of the treatments (N, N+S, N+K) rather than from significant changes in K concentration. Overall, our results suggest that K availability was adequate for all species at most of our study sites. However, K deficiencies are probably common on other soil and parent material types in the inland Northwest (Mika and Moore 1991, Mandzak and Moore 1994, Moore and Mika 1997).

In order to evaluate how foliar nutrient analysis compared to growth response, we analyzed four-year volume response to the fertilizer treatments for the mixed conifer stands. Four-year growth responses generally confirm the foliar nutrient response results for the four tree species. Douglas-fir showed significant growth increase to the N+S treatment but not to the N-only treatment, suggesting that S availability was inadequate for Douglas-fir on these sites. While Douglas-fir has been found by others to show good growth response to N-only fertilization on many sites in the inland Northwest (Moore et al. 1991, Shafii et al. 1990, Shafii et al. 1989), perhaps S deficiencies explain some of the variation in response they observed. Both N-only and N+S treatments produced significant growth response for grand fir, but there was no significant difference between treatments. This indicates a probable deficiency in N but not S for grand fir. Other studies have found that grand fir was likely to show a strong growth response to N fertilization (Chappell and Bennett 1993, Scanlin and Lowenstein 1979), and similar results have been reported for other true firs (Powers 1979, Powers 1983, Cochran 1991). In our study, lodgepole pine showed significant growth response to N and N+K fertilization, but not to N+S. Although 25% of the lodgepole pine sites responded very poorly to N+S fertilization, another 25% responded very well. The reasons for this variation in response to N+S by lodgepole are unclear, but it does appear that volume response to N+S fertilization greatly depends on site-specific factors. Brockley (1995) attributed inconsistent growth responses of several lodgepole pine sites to variation in foliar S status following N fertilization. Binkley et al. (1995) found variation in growth response of lodgepole pine by stand age, with older stands showing strong growth responses and young stands showing no significant growth responses to fertilization. Both studies may help explain our results, as our lodgepole pine sites covered a range of stand ages and a potential range of S availability.

Ponderosa pine did not respond significantly to any of the fertilizer treatments. Ponderosa pine has been shown to respond to N, P and S fertilization on some sites (Cochran 1978, 1973). The non-responding sites on those studies were drier sites, where moisture was thought to be a limiting factor to growth. While some of the ponderosa sites on our study occurred on relatively dry PSME sites on the Okanogan N.F., those growth responses did not differ significantly from the wetter ABGR sites of the Umatilla N.F., indicating that moisture was not a limiting factor. Weetman et al. (1988) found that for lodgepole pine, volume response to fertilization was weak where nutrients were adequate, indicating that some other factor was controlling response. Ponderosa pine nutrient status appeared to be adequate for N and K on our study sites based on foliar nutrient levels, which likely explains the subsequent lack of growth response to the fertilizer treatments. Ponderosa pine may be better able to obtain adequate nutrients, or perhaps it has lower nutrient requirements, than the other conifer species we studied. In terms of its evolutionary history, ponderosa pine has developed in a fire-dependent ecosystem, where nutrients were cycled back to an available form on a frequent basis, which may explain why ponderosa has lower nutrient requirements than other species. Ponderosa pine may have evolved an inability to exploit less-available nutrient sources or to retain nutrients for long-term storage and use. Ponderosa pine may therefore be at a competitive disadvantage with other species sharing the same site, thus explaining the low volume growth response to fertilization and nutrient uptake observed in our mixed conifer study sites.

Conclusions

Douglas-fir showed both N and S deficiencies in foliage samples, and produced significant growth response to the N+S treatment. However, Douglas-fir did not respond significantly to the N-only fertilization, possibly due to concurrent S limitations. Grand fir produced significant growth response to both N-only and N+S treatments of about the same magnitude, despite low foliar S levels. This result suggests that N was the primary limiting nutrient, and that as opposed to Douglas-fir, grand fir was better able to utilize N even while S was at deficiency levels. Foliar analysis for lodgepole pine suggested that N, S, and sometimes K concentrations were inadequate. The N-only and N+K treatments produced significant lodgepole pine growth responses of similar magnitude. However, lodgepole pine response to the N+S treatment was highly variable across our study sites. Ponderosa pine did not show nutrient deficiencies for N or K, and did not respond significantly in either foliar K or S levels or in growth to N, N+K or N+S fertilization. This suggests that nutrient deficiency may not have been a factor limiting foliar nutrient response and growth for ponderosa pine.

Nitrogen was the most commonly deficient nutrient across all species and sites, followed by S. Foliar N levels increased significantly following N fertilization for all species. In contrast, insignificant increases in foliar S levels occurred following N+S fertilization for Douglas-fir and grand fir, and no changes in foliar S occurred for the pines. Given both this species-related variation in response and the possibility of induced S deficiencies caused by N fertilization, additional experimentation using higher rates of S fertilization is suggested. Along with S rate studies, additional work on determining critical and optimal foliar S levels for northwest conifer species is necessary. In our study, K availability seemed adequate based on initial K levels and the low response of foliar K to N+K fertilization. However, K may be commonly deficient on other soil and parent material types in the region, and continuing work on the K-supplying capability of various parent material types and the role of K in northwest conifers' physiological processes should be continued.

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