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Foliar nutrient and tree growth response of mixed-conifer stands to three fertilization treatments in northeast Oregon and north central Washington

Mariann T. Garrison*, James A. Moore, Terry M. Shaw, Peter G. Mika

Intermountain Forest Tree Nutrition Cooperative, Forest Resources Department,
University of Idaho, Moscow, ID 83844-1133, USA

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Abstract

The results of two studies evaluating nutrient uptake in mixed-conifer stands following fertilization are reported. The four species examined were Douglas-fir, grand fir, lodgepole pine and ponderosa pine. The fertilization treatments were 224 kg ha^{-1} nitrogen, 224 kg ha^{-1} nitrogen plus 112 kg ha^{-1} sulfur, and 224 kg ha^{-1} nitrogen plus 190.4 kg ha^{-1} potassium. Foliar nutrient concentrations, contents and ratios were analyzed, as well as four-year volume response. Douglas-fir showed both N and S deficiencies in control foliage samples, and produced significant growth response to the N + S treatment, but not to the N-alone treatment. Grand fir also showed foliar N and S deficiencies, but produced significant growth response to both N and N + S fertilization. This suggests that grand fir was better able to utilize N than Douglas-fir even under S-limiting conditions. Lodgepole pine showed deficient foliar N and S concentrations, and produced significant volume responses to N and N + K fertilization. Lodgepole volume response to N + S fertilization was highly variable, and appeared to be site-specific. 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. © 2000 Elsevier Science B.V. All rights reserved.

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1. 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 menziesii* (Douglas-fir), *Abies grandis* (grand fir), *Pinus contorta* (lodgepole pine), and *Pinus ponderosa* (ponderosa pine). The fertilization treatments were nitrogen (N), nitrogen with potassium (N + K), and nitrogen with sulfur (N + S). One intent of the research was to determine

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* Corresponding author. Tel.: +1-208-885-4033;
fax: +1-208-885-6226.
E-mail address: mariang@novell.uidaho.edu (M.T. Garrison)

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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 (Cochran, 1978; Powers, 1983; Shaffi et al., 1989; Mika and Moore, 1991; Moore et al., 1991; Brockley, 1995).

2. Methods

2.1. Study area

A total of 16 sites were established, eight each on the Umatilla (northeastern Oregon) and Okanogan (central Washington) National Forests. The stands ranged in age from 11 to 40 years old at the time of fertilization, with the exception of one Okanogan site, which was ca. 70 years old. All were second growth stands, some were naturally regenerated and some planted. Foliage samples were collected from one or two species per site, based on species abundance and distribution throughout the stand. Elevations ranged from 885 to 1675 m asl. Vegetation series (Johnson and Clausnitzer, 1992; Williams and Lillybridge, 1983) included subalpine fir (ABLA), Douglas-fir (PSME), and grand fir (ABGR). The climate of the study areas is characterized by mild, moist winters resulting from Pacific maritime influences and dry warm summers. Atmospheric depositions of N and S are relatively low as the study areas are well removed from population centers. Basaltic, granitic and glacial till rock types were included in the study. Elevation, vegetation series, rock type, dominant species, and stand characteristics are provided for each study site in Table 1.

2.2. Design and treatments

The Umatilla and Okanogan studies were established in 1991 and 1993, respectively. A study site, or installation, consisted of six 0.112 ha square plots, each surrounded by a 6.1–12.2 m buffer strip. To reduce among-plot variation, plots were grouped into two blocks of three plots based on similarity in terrain,

Table 1
Site and stand characteristics for 16 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[a]

Site	Elevation (m)	Veg. series	Parent material	Species studied	BA (m^2/ha)	DBH (cm)
Umatilla N.F.						
313	1675	ABLA	Basalt	GF/LP	15	13
314	1525	ABGR	Basalt	DF/GF	11	11
315	1370	ABGR	Basalt	GF/PP	23	21
316	1675	ABGR	Basalt	GF/PP	18	18
317	1455	ABGR	Basalt	DF/LP	1	3
318	1465	ABGR	Basalt	PP	1	3
319	1465	ABGR	Basalt	DF/PP	1	3
320	1465	ABGR	Basalt	PP	5	7
Okanogan N.F.						
327	1025	PSME	Tonalite	PP	22	21
328	1585	ABLA	Ash/Glacial Till	LP	11	14
329	1675	PSME	Granodiorite	LP/PP	4	7
330	885	PSME	Ash/Glacial Till	PP	24	26
331	1585	ABLA	Glacial Till/Granite	LP	10	14
332	1510	ABLA	Glacial Till/Granite	LP	8	7
333	1295	ABLA	Ash/Glacial Till	LP	8	8
334	1235	PSME	Glacial Till/Lacustrine	LP	23	18

[a] Note: Habitat classification is given as vegetation series (Veg. Series). Stand mensurational information includes basal area (BA, m^2/ha) and diameter at breast height (DBH, cm).

vegetation composition, tree stocking, and tree size. Fertilizer treatments were randomly assigned to the plots within each block.

In each block, one plot remained untreated, serving as a control, and one plot was treated with 224 kg ha^{-1} N. In the Umatilla study, the third plot was treated with 224 kg ha^{-1}N + 112 kg ha^{-1} S (N + S) while, in the Okanogan study, the third plot was treated with 224 kg ha^{-1} N + 190.4 kg ha^{-1} K (N + K). Red potash (KCl) supplied the K, ammonium sulfate supplied the S, and urea supplied the N except for the N + S treatments where a portion was supplied by ammonium sulfate. Fertilizers were applied in the fall of the establishment year.

2.3. Measurements and laboratory analysis

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. All plot trees were measured. Volumes were calculated using species-specific 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).

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 based on percent basal area in the stand, 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 four foliage samples per treatment if one species was sampled, and eight per treatment if two species were sampled, resulting in totals of 12 and 24 foliage sample trees per installation, respectively. Analysis of between-tree variation in Douglas-fir foliar nutrient concentration using foliage samples of 1020 trees from 85 sites had indicated that four trees per treatment were sufficient to adequately estimate concentration levels (IFTNC, unpublished data). 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°C for 24 h, needles were separated from stems, and the separated needles were re-dried at 70°C for another 24 h. 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.

3. Data analyses

3.1. 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, 1978; 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, 1978; 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. 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, 1978). A foliar N/S ratio below 14.7 suggests that sufficient S is present for proper N utilization. A foliar

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[e]	1.15[g]	1.20[e]	1.10[g]
P (%)	0.12[e]	0.15[g]	0.12[e]	0.08[g]
K (%)	0.60[e]	0.58[f]	0.50[e]	0.48[f]
S (%)	0.11[f]	0.08[h]	0.09[h]	0.08[h]
Ca (%)	0.15[e]	0.12[f]	0.08[e]	0.05[f]
Mg (%)	0.08[e]	0.06[f]	0.09[e]	0.05[f]

[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.

[e] Values obtained by: best estimate by cited author based on literature review and personal experience.

[f] Values obtained by: derived by cited author using optimal proportions.

[g] Values obtained by: derived by cited author experimentally.

[h] Values obtained by: 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, 1978).

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 (Ingestad, 1967, 1979) suggested that for all conifers a foliar K/N ratio of 0.50 is critical, while a ratio of 0.65 is optimal.

For each of the four species studied, the following foliar nutrient variables were examined: foliar concentration (%) and content (needle weight × % concentration) for N, K, and S, as well as N/S and K/N ratios. The values for each nutrient variable were averaged for the four trees sampled for each species and each treatment. These mean values per treatment 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 $p = 0.10$ (Lehman, 1975; Kim and Jennrich, 1973; Kim, 1969). The critical foliar nutrient concentrations or ratios are shown in Table 2 and represented by vertical lines in the figures.

3.2. Volume growth response

To minimize scaling problems due to differences in tree size, and thus better assess the effects of fertilization on tree growth, we calculated the volume response of each fertilized plot relative to the control plot. First, using a method similar to Powers et al. (1985), we calculated gross relative volume growth for the four-year period following fertilization for each species and plot, using Eq. (1):

$$\mathrm{RVG}\,(\%) = \frac{(\mathrm{GV}_4 - \mathrm{GV}_0)}{\mathrm{GV}_0} \times 100 \tag{1}$$

where RVG is the gross volume growth at year 4 relative to initial volume (year 0), calculated for each plot and species, and GV is the gross volume at year 0 (GV_0) and at year 4 after fertilization (GV_4).

We then used the gross relative volume growth of the control plot to determine the relative volume responses of the two fertilization treatments for each block, using Eq. (2):

$$\mathrm{RVR}_\mathrm{F}\,(\%) = \frac{(\mathrm{RVG}_\mathrm{F} - \mathrm{RVG}_\mathrm{C})}{\mathrm{RVG}_\mathrm{C}} \times 100 \tag{2}$$

where RVR is the volume response of the fertilized plots relative to control plot growth, calculated for the two fertilization treatments within each block at each installation, and RVG is the relative volume growth of the fertilized (RVG_F) and control (RVG_C) plots calculated using Eq. (1).

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 0 response level on the horizontal axis. The Kolmogorov–Smirnov criterion was again used to test for differences between distributions for various treatments ($p = 0.10$), 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.

4. Results

4.1. Douglas-fir

4.1.1. 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 Fig. 1(a). Without fertilization, all of the sites tested were deficient in N. Application of N fertilizer increased N concentrations on all sites, with the magnitude of response depending on treatment. The greatest response in foliar N levels occurred when N was applied as urea, with all sites 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. 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.

Trees on control and N-alone treatments had below-critical foliar S concentrations at all sites, with no apparent difference in S uptake by treatment for Douglas-fir on the Umatilla N.F. (Fig. 1(b)). The N + S treatment produced somewhat higher S concentrations than the control and N-alone treatments, however only one site had above-critical S levels. Although not shown, foliar S content paralleled the results for Douglas-fir S concentration. The distributions portrayed in Fig. 1(b) did not differ significantly from each other; however, there appeared to be some S uptake on the N + S treatments.

All of the Umatilla Douglas-fir controls had excessive foliar N/S ratios (Fig. 1(c)). Following fertilization with N alone, foliar N/S ratios were significantly higher. Following N + S fertilization, the N/S ratios were excessive on only 70% of the sites, and did not differ significantly from control levels.

4.1.2. Foliar potassium response and potassium/nitrogen ratios

Foliar K concentrations of Douglas-fir on the Umatilla were above critical for all sites and treatments. The three treatments produced no significant differences in foliar K concentration or content (distributions not shown).

As noted previously, 0.50 and 0.65, respectively, are considered critical and optimum K/N ratios for most conifer species, and these values are depicted in Fig. 1(d) along with foliar K/N ratio distributions for the Umatilla N.F. Douglas-fir. Foliar K/N ratios on the control treatments were always above critical, and above optimal ca. 70% of the time. Following N-only fertilization, K/N ratios were significantly lower, decreasing to sub-critical levels on all sites. Following N + S fertilization, foliar K/N ratios were above critical on all sites, and above optimal ca. 70% of the time. Overall, when S was applied along with N fertilization, a better K/N ratio was maintained.

4.1.3. Growth response of fertilized Douglas-fir

Volume growth for Douglas-fir tended to increase in response to both N and N + S during the four years following fertilization, with the N + S treatment producing the best growth response. The four-year volume growth response of Douglas-fir on the N-treated plots was positive ca. 70% of the time (Fig. 1(e)), but the average response was not significantly greater than 0. 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.

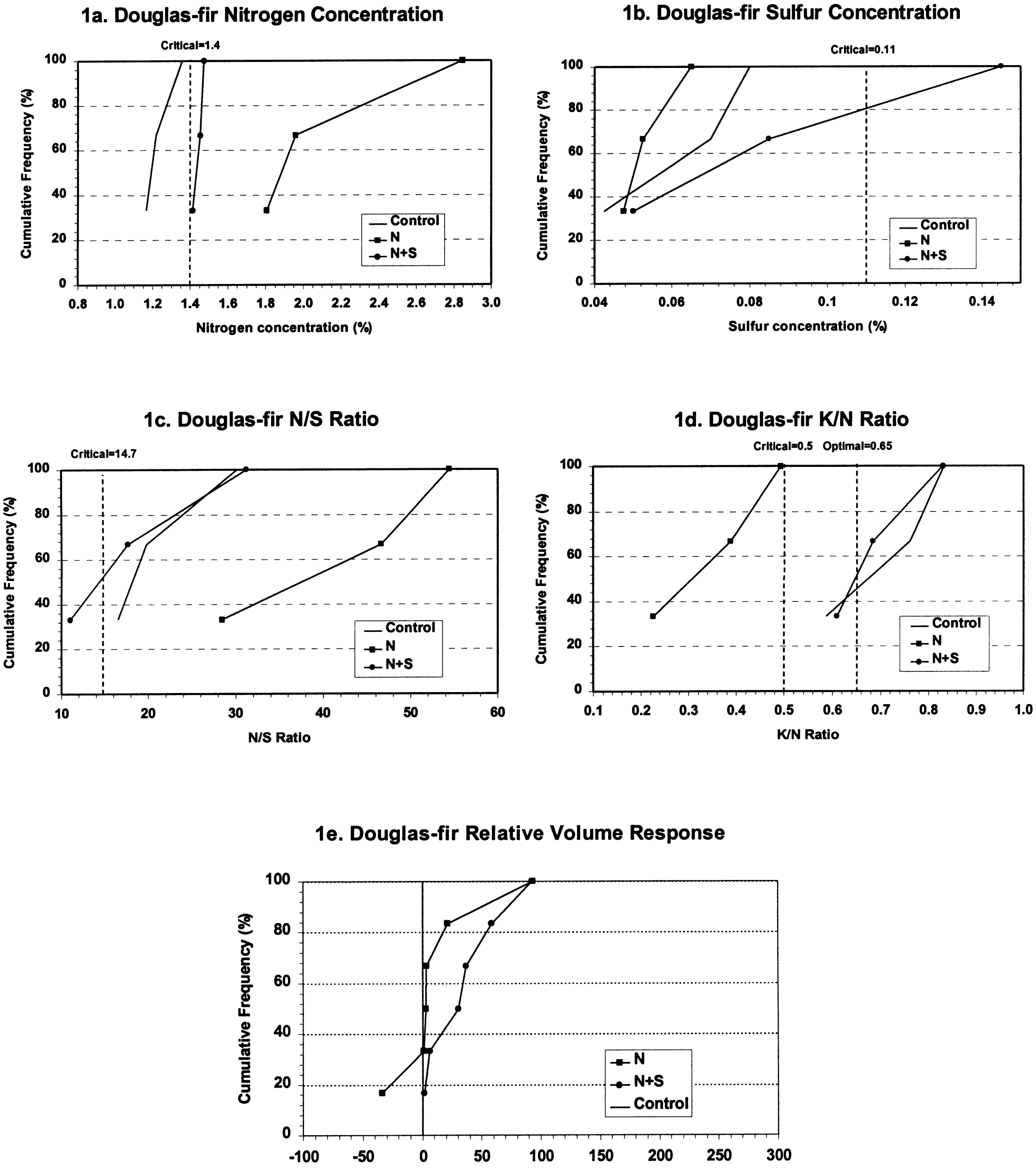


Fig. 1. Relative frequency distributions of foliar nutrient levels and four-year volume response for Douglas-fir following fertilization with 224 kg ha^{-1} N (N) and 224 kg ha^{-1} N + 112 kg ha^{-1} S (N + S) on the Umatilla National Forest in northeastern Oregon and southeastern Washington. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content, ratio or volume response given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. For relative volume responses, control levels are set to 0 and also indicated by a vertical line.

4.2. Grand fir

4.2.1. Foliar nitrogen, sulfur and potassium concentrations

Cumulative distributions of grand fir foliar N concentrations by treatment for four sites on the Umatilla National Forest are shown in Fig. 2(a). Untreated trees on most sites had foliar N concentrations below critical levels. Following application of both N and N + S, all sites 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 for all treatments (distributions not shown). Furthermore, there were no significant differences in foliar K concentration between any of the treatments. Grand fir foliar K/N ratios also remained above the critical value for essentially all sites regardless of treatment.

Foliar S concentrations for untreated grand fir were below critical levels on all sites (Fig. 2(b)). Seventy-five percent of the sites receiving the N-only treatment showed S concentrations below critical one year after fertilization, while half of the sites receiving the N + S

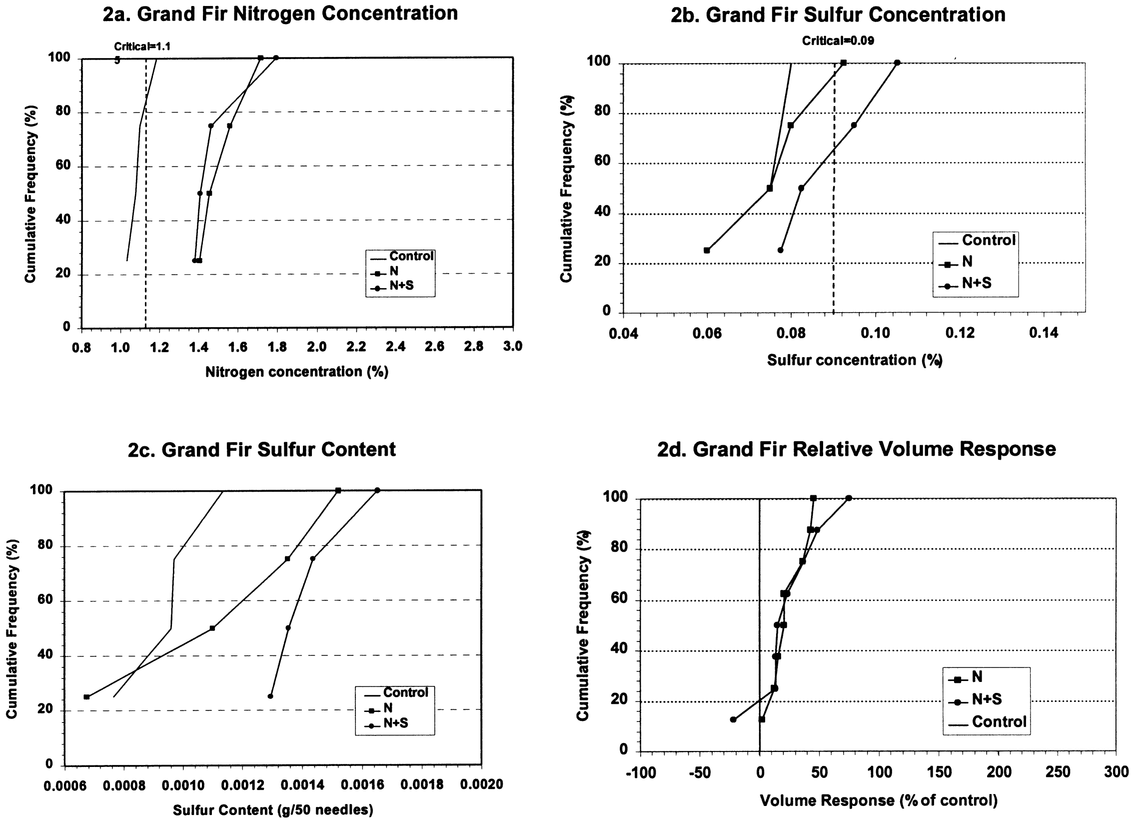


Fig. 2. Relative frequency distributions of foliar nutrient levels and four-year volume response for grand fir following fertilization with 224 kg ha^{-1} N (N) and 224 kg ha^{-1} N + 112 kg ha^{-1} S (N + S) on the Umatilla National Forest in northeastern Oregon and southeastern Washington. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content, ratio or volume response given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. For relative volume responses, control levels are set to 0 and also indicated by a vertical line.

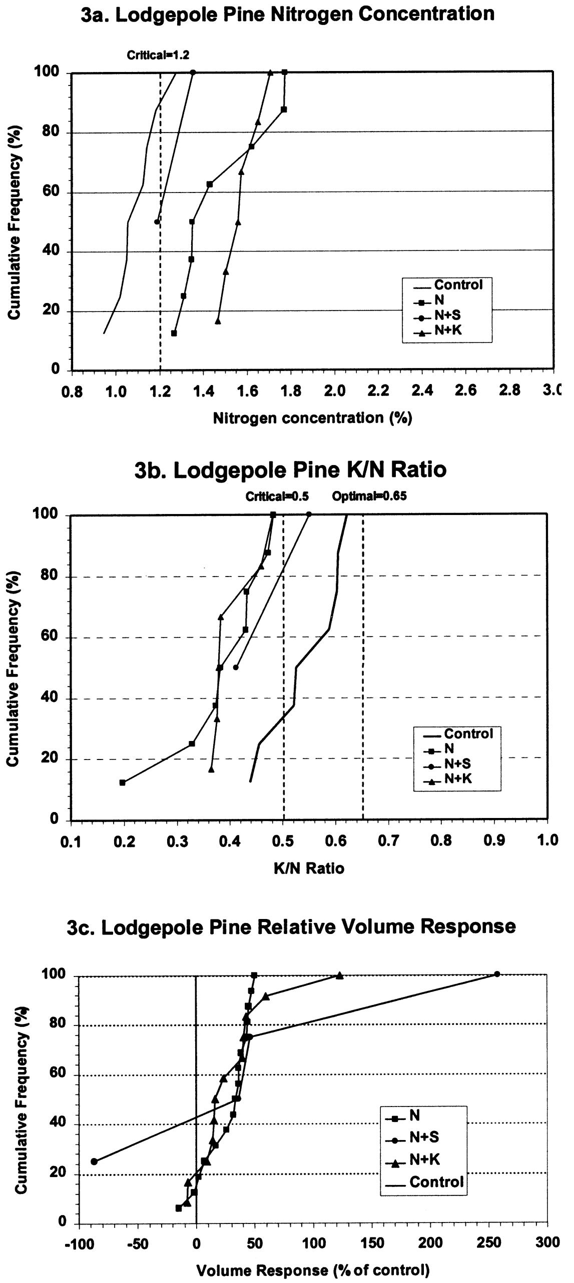


Fig. 3. Relative frequency distributions of foliar nutrient levels and four-year volume response for lodgepole pine following fertilization with 224 kg ha^{-1} N (N) and 224 kg ha^{-1} N + 112 kg ha^{-1} S (N + S) on the Umatilla National Forest in northeastern Oregon and southeastern Washington, and 224 kg ha^{-1} N (N) and 224 kg ha^{-1} N + 190.4 kg ha^{-1} K (N + K) fertilization on the Okanogan National Forest in north central Washington. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content, ratio or volume response given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. For relative volume responses, control levels are set to 0 and also indicated by a vertical line.

treatment had concentrations above the critical level. The N-only foliar S concentrations were not significantly different from the controls. The N + S sites, however, showed higher S concentrations than the N-alone and control sites, suggesting that S uptake occurred when S was applied with N. Foliar S contents for grand fir (Fig. 2(c)) showed that trees receiving N + S fertilization had significantly greater foliar S contents than untreated trees on all sites, confirming S uptake. This result was also apparent from the N/S ratios (not shown), wherein the N/S ratios were generally better (lower) on the N + S than on the N-alone sites.

4.2.2. 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 (Fig. 2(d)). 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.

4.3. 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.

4.3.1. Foliar nitrogen and potassium concentrations and K/N ratios

The relative cumulative frequency diagram for lodgepole pine foliar N concentrations shows that unfertilized trees were N deficient on ca. 90% of the unfertilized sites (Fig. 3(a)). Foliar N concentrations increased to above-critical levels after application of all three fertilizer treatments, but the increase was not significant for the N + S treatment.

Lodgepole pine treated with N-only had foliar K concentrations below critical levels ca. 35% of the time (distribution not shown) Essentially all other treatments produced K concentrations above critical levels. Lodgepole pine receiving N + K treatments had significantly higher foliar K content than unfertilized trees, confirming K uptake.

Lodgepole pine controls showed the best foliar K/N ratios, with 75% of the sites above the critical level (Fig. 3(b)). One year following fertilization all of the N-alone and N + K treatments had K/N ratios below the critical level. Following N + S fertilization, most of the sites also showed sub-critical K/N ratios, and all were below the optimal ratio.

4.3.2. Foliar sulfur concentrations and N/S ratios

Foliar S concentrations were below critical for lodgepole pine on all control and fertilized treatments. 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 for those trees that received the N + S treatment.

All Umatilla N.F. lodgepole pine study sites had excessive N/S ratios, regardless of whether they received fertilization. Although the control trees had the better (lower) N/S ratios compared to treated trees, they also tended to be N-deficient, indicating a probable nutrient imbalance on these sites. Trees 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 trees, the high ratio is not of great concern. Trees receiving N + S showed a better N/S balance than those receiving N-alone, but the lower N concentrations for this treatment compared to N-only indicate a potential nutrient imbalance.

4.3.3. Growth response of fertilized lodgepole pine

Growth responses for both the N-alone and N + K fertilization were significantly greater than the control, though they were not significantly different from each other (Fig. 3(c)). This indicated 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 0, nor did it differ significantly from the N and N + K treatments. The N + S treatment did, however, produce both the most negative response and the highest positive response observed in this study.

4.4. Ponderosa pine

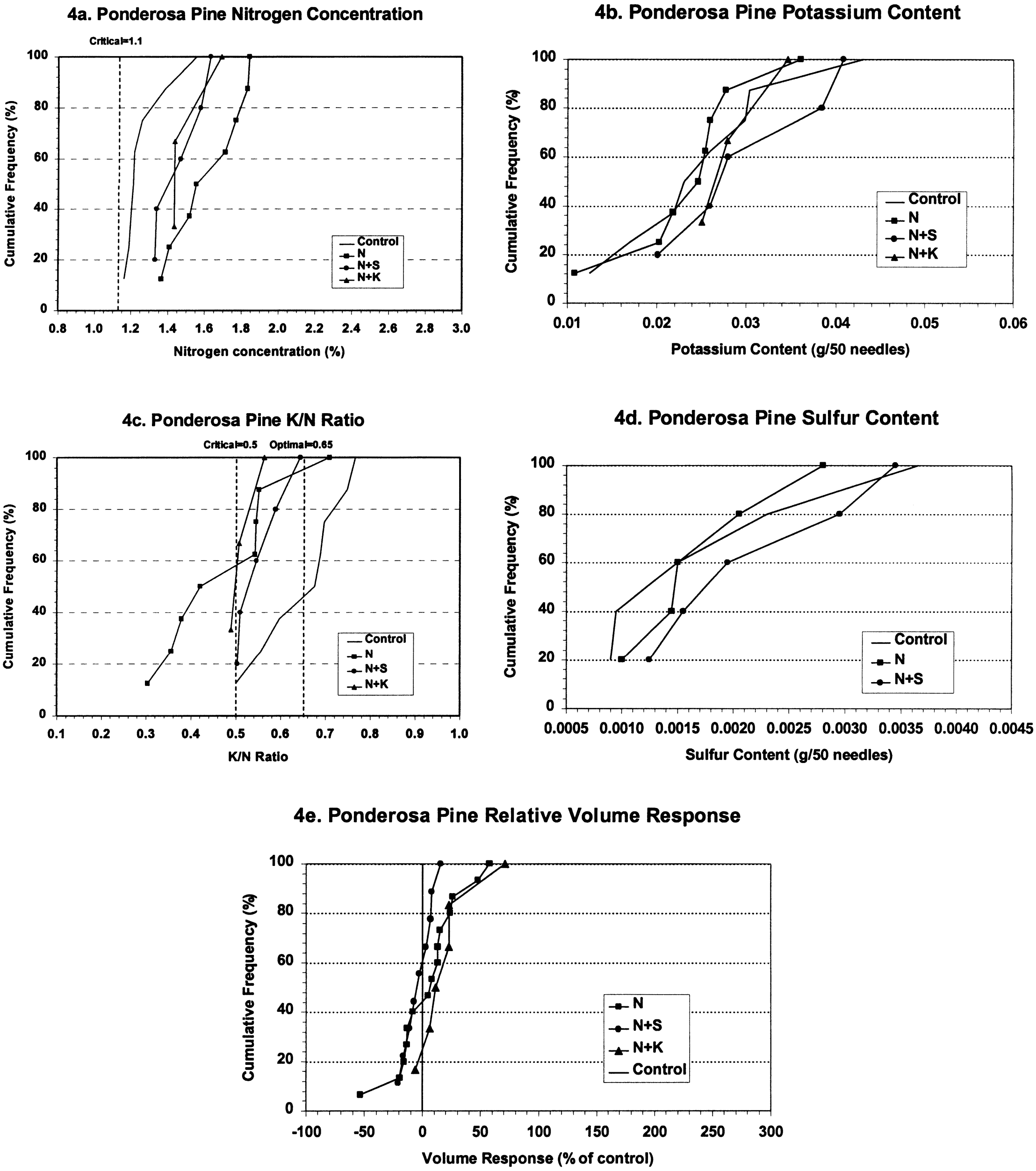
Ponderosa pine occurred on five installations on the Umatilla Forest, and on three sites on the Okanogan Forest. As with lodgepole pine, analysis of variance for ponderosa pine showed that nutrient concentrations and responses did not differ between the National Forests, allowing us to combine these 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.

4.4.1. Foliar nitrogen and potassium concentrations and K/N ratios

Foliar N concentrations for ponderosa pine growing in unfertilized mixed-conifer stands were always above published critical levels (Fig. 4(a)). One year after fertilization, all of the fertilized treatments had foliar N concentrations significantly greater than control levels, indicating that N uptake did occur during the first growing season after treatment. The N-alone treatment produced the highest foliar N concentrations, while the N + K and N + S treatments were similar to each other. Compared to published critical levels (Table 2), N was not deficient for ponderosa pine in mixed-conifer stands. However, the trees took up applied fertilizer N; this was reflected in foliar N contents as well (graph not shown).

Ponderosa pine foliar K concentrations were above critical levels for all treatments, with no significant differences between the controls and any treatment for K concentration (graph not shown). The N + S treatment produced significantly greater K content compared to the controls (Fig. 4(b)). These results indicated that ponderosa pine in mixed-conifer stands did not take up applied fertilizer K, and the addition of N with or without K did not affect K uptake.

Foliar K/N ratios for ponderosa pine were above critical (0.50) on most of the controls, and above optimal (0.65) on over 50% of the controls (Fig. 4(c)). Following fertilization with N alone, foliar



4a. Ponderosa Pine Nitrogen Concentration

4b. Ponderosa Pine Potassium Content

4c. Ponderosa Pine K/N Ratio

4d. Ponderosa Pine Sulfur Content

4e. Ponderosa Pine Relative Volume Response

Fig. 4. Relative frequency distributions of foliar nutrient information and four-year volume response for ponderosa pine following fertilization with 224 kg ha^{-1} N (N) and 224 kg ha^{-1} N + 112 kg ha^{-1} S (N + S) on the Umatilla National Forest in northeastern Oregon and southeastern Washington, and 224 kg ha^{-1} N (N) and 224 kg ha^{-1} N + 190.4 kg ha^{-1} K (N + K) fertilization on the Okanogan National Forest in north central Washington. The vertical axis indicates the proportion of all installations with values less than or equal to a particular nutrient concentration, content, ratio or volume response given on the horizontal axis. Critical nutrient concentrations and critical or optimum nutrient ratios are indicated by vertical lines at the appropriate level. For relative volume responses, control levels are set to 0 and also indicated by a vertical line.

K/N ratios were below critical on 50% of the sites, and below optimal ca. 90% of the time. Following N + K as well as N + S fertilization, foliar K/N ratios were above critical but below the optimal ratios. The foliar K/N ratios for ponderosa pine were highest on controls, primarily reflecting their low N concentrations. Foliar K/N ratios were the next highest on the N + S treatments, due to increased K uptake and decreased N uptake relative to the other fertilizer treatments. Foliar K/N ratios were lowest (worst) on N-alone treatments, a result of high foliar N concentrations.

4.4.2. *Foliar sulfur concentrations and N/S ratios*

Foliar S concentrations for ponderosa pine were deficient on 90% of the controls, and on all of the N and N + S fertilization treatments (graph not shown). Overall, the N and N + S treatments had no significant effect on foliar S concentrations. However, foliar S content (Fig. 4(d)) did increase on the N + S treatments, 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. Since foliar N concentrations for ponderosa pine were above the critical level on all of the ponderosa pine sites, regardless of whether they were fertilized (Fig. 4(a)), the high N/S ratio does not necessarily indicate an imbalance.

4.4.3. *Growth response of fertilized ponderosa pine*

Relative volume growth response of ponderosa pine after four years was marginally significant ($p = 0.1$) only for the N + K treatment compared to the controls (Fig. 4(e)). None of the other treatments differed significantly from each other or from the controls. Overall, 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.

5. Discussion

Without fertilization, Douglas-fir on all sites showed inadequate foliar N concentrations. Most unfertilized grand fir and lodgepole pine also showed inadequate foliar N, while most ponderosa pine foliage samples were above critical N levels. While this in part reflects the lower nutrient requirements of ponderosa compared to the other three species studied, it also suggests that ponderosa pine growing in mixed-conifer stands were able to obtain adequate N when the other three conifers were unable to do so. After fertilization with N-only, all four species had above critical foliar N on all sites. Nitrogen uptake was uniformly good for all species after treatment with urea at a rate of 224 kg N ha^{-1}. 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, the N-only treatment consistently produced the highest N concentrations. 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 type effect, since N + S supplied a portion of the N in ammonium sulfate form, while the other two treatments supplied 100% of the N as urea. Urea temporarily increases soil pH, which may increase the effectiveness of ammonium uptake, and conversely ammonium sulfate causes a decrease in pH, which may decrease the effectiveness of ammonium uptake (Tisdale et al., 1985). Brockley (1995) found that while different fertilizer N sources resulted in different first year foliar N concentrations for lodgepole pine, the growth of the same trees was not affected by the different N source.

For all species, most unfertilized trees 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. However, analysis of foliar S contents confirmed that S uptake did occur on the N + S treatments for grand fir, Douglas-fir and ponderosa pine, and this increase was significant for grand fir and ponderosa pine. This result suggests that the lack of foliar S concentration response for these species was a growth dilution effect. Lodgepole pine did not show any changes in foliar S content or concentration following fertilization.

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, 1978; Turner et al., 1977, 1979; Turner, 1979). Turner and Lambert (1978) 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 treatments for any of the four species showed adequate N/S ratios. These results suggest that our sites are 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 species. Foliar N/S ratios following N + S fertilization did not differ significantly from the controls for any of the four species, although 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 3–4 year growth response tended to be greater on the 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 fertilized sites. In our study, foliar S contents of Douglas-fir, grand fir and ponderosa pine increased on N + S treatments, suggesting growth dilution did occur. Tiedemann et al. (1998) reported that soil S availability was depressed following fertilization with urea at a rate of 350 kg ha^{-1} N, and recommended the addition of S with N fertilization. Our S content results did not show decreased S availability following N application, but this was probably due to both lower application rate (224 kg ha^{-1} N) and the fact that the N was partially supplied by ammonium sulfate rather than urea. We did, however, find that S uptake was greater on the N + S treatments than the N-alone or untreated plots, and therefore support the recommendation that S be supplied with N fertilization.

All unfertilized sites for all four species showed foliar K concentrations above adequate levels. 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 increased significantly for lodgepole pine following application of N + K fertilizer. Foliar K contents also increased significantly for the N + S treatment over N-alone for ponderosa pine. This K response 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 influx of NH_4^+ ions from ammonium-based fertilizers has been shown to compete with K^+ ions for sites on the soil exchange complex (Liu et al., 1997; Chen et al., 1989). In our study, this appears to have resulted in an increase in exchangeable K available for plant uptake. This may also explain the lower foliar N response of those sites, as 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 ions.

The balance of foliar K and N (K/N ratio) is also important (Mika and Moore, 1991). Unfertilized trees generally showed adequate balance. After fertilizing with N-only, all species except grand fir showed a significant decline in foliar K/N ratios, with 90% of the Douglas-fir and all of the lodgepole pine sites 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).

Four-year growth responses generally confirmed the foliar nutrient response results for the four tree species. Douglas-fir showed significant growth response 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; Shaffi et al., 1990, 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 (Tiedemann et al., 1998; Chappell and Bennett, 1993; Scanlin and Loewenstein, 1979), and similar results have been reported for other true firs (Powers, 1979, 1983; Cochran, 1991). Based on soil tests and bioassay studies, Tiedemann et al. (1998) suggest that on sulfur-deficient soils, N and S should be applied together to ensure S availability and future yields.

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 in Cochran's 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 (Monleon and Cromack, 1996; Covington and Sackett, 1984). As such, 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 low nutrient uptake observed in our mixed-conifer study sites.

An interesting phenomenon regarding species ecology and nutrient uptake has suggested itself over the course of this study. Generally speaking, we found that the shade-tolerant species (grand fir, Douglas-fir) took up more nutrients than shade intolerants (lodgepole and ponderosa pines). While information on comparable species mixes was not found, other workers comparing mixedwood and spruce stands found that the more tolerant spruce stands held significantly greater amounts of nutrients in the standing crop than did the mixedwood (Gordon, 1984). A comparison of spruce, larch and pine by Miller et al. (1993) showed that spruce took up the most nutrients, followed by pine, and then larch. This same sequence also reflects tolerance levels: spruce is the most tolerant, followed by pine, and larch is the most intolerant (Harlow et al., 1979). Alban (1982) compared spruce and pine nutrient uptake rates, and found that the spruce took up more nutrients than pine, and that these uptake rates were reflected in the litterfall. This differentiation in nutrient uptake rates makes sense as a competitive strategy for the shade tolerants, as a means of attaining the nutrients needed to overtake the intolerant overstory. This may also relate to the ponderosa pine fire-dependency mechanisms mentioned previously. Under normal frequent-fire conditions, the tolerant and nutrient-demanding understory species would not survive to compete with the intolerant pine, hence the pine would not have needed to develop competitive mechanisms for nutrient uptake.

6. 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 show a significant growth response following 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. 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 current 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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