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The effect of multi-nutrient fertilization on understory vegetation nutrient concentrations in inland Northwest conifer stands

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Abstract

This study looked at the effects that multi-nutrient fertilization had on understory vegetation nutrient concentrations at four conifer forested locations in the inland Northwest. Multi-nutrient fertilization of conifer stands cannot only enhance the overstory species in the inland Northwest but also the understory vegetation. Determination of nutrient concentration response to fertilization treatments can provide managers the ability to better manipulate their forests for grazing and wildlife habitat. We grouped the understory vegetation into three general life forms: forbs, grasses and grass-likes, and shrubs. Multi-nutrient fertilization had little effect on nitrogen concentration across all life forms. Potassium and sulfur generally increased in concentration. Micronutrients as a whole showed less variability in response to multi-nutrient fertilization. Boron, copper, molybdenum, and zinc generally showed increases in concentrations across all life forms. We were able to conduct analyses on a selected number of understory vegetation species. Individual species showed variability in nutrient concentration response to multi-nutrient fertilization. Wildlife habitat and grazing quality were both increased and decreased following multi-nutrient fertilization. Increases in nutrient concentrations will provide more nutritious vegetation to these animals and vice versa for decreases in concentrations.
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1. Introduction

Forest fertilization may be an effective treatment to increase or maintain multiple resource outputs on a land base that is declining because of urbanization and government regulation. Most forests in the inland Northwest are nutrient deficient and overstory conifers respond with increases in growth (Shaffii et al., 1989; Moore et al., 1991; Garrison et al., 2000) and changes in nutrient concentrations following fertilization (Garrison et al., 2000). However, information regarding fertilization effects on understory vegetation nutrient concentrations in the inland Northwest is minimal. Nutrient concentration and contents for individual species differs from biomass because species with a low number of plants or a low amount of biomass can still have a large impact on the ecosystem. Different understory species uptake varying amounts of individual nutrients (Tappeiner and Alm, 1975; Grime, 1977; Turner et al., 1978; Chapin et al., 1986; Meerts, 1997). Therefore, a species with a low amount of occurrence (whether number or biomass) may uptake

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large amounts of boron (B), for instance, making it very important in terms of the nutrient cycle for that site (Tappeiner and Alm, 1975; Turner et al., 1978). This makes quantifying response of understory vegetation to multi-nutrient fertilization very important. Determining understory concentration response to multi-nutrient fertilization can also affect conifer stand management for wildlife and domestic animals.

Several studies have shown that fertilization changes nutrient concentrations of understory vegetation in conifer stands across the United States. Nitrogen (N) concentration of elk sedge (*Carex geyeri* Boott) increased following an N application in a ponderosa pine (*Pinus ponderosa* Dougl.) stand in eastern Oregon (Riegel et al., 1991). Prescott et al. (1993) reported results for salal (*Gaultheria shallon* Pursh) of what could be considered three different fertilization studies conducted in mature second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) stands in Washington. In two studies, fertilization resulted in greater concentrations of N and sulfur (S), and lower concentrations of potassium (K) in salal. In a third study, S-only and S combined with N fertilization treatments resulted in increases in salal S concentration, but N-only and N combined with S fertilization treatments produced mixed results. Wood (1986) found that N and phosphorus (P) fertilization did not affect N concentration for understory vegetation shrubs in loblolly pine (*Pinus taeda* L.) and longleaf pine (*Pinus palustris*) stands in South Carolina. In another study conducted in loblolly pine in North Carolina, most ground cover species had higher N concentrations following N, P, and K fertilization, while P and K did not produce clear trends across all species (Haines and Haines, 1979). Tiarks and Haywood (1986) found that N and K concentrations were not affected following N, P, and K fertilization in herbaceous plants in a loblolly pine plantation in Louisiana. Several years after fertilization with N and P in a Florida slash pine plantation, Wood and Tanner (1985) found increased N concentrations in one species. These studies show mixed results and it is unclear if fertilization will always increase nutrient concentration amounts in understory vegetation.

Soil nutrition can influence understory vegetation composition. Sites with limiting nutrient amounts usually contain understory plants/species that require lower amounts of nutrients to grow (Grime, 1977; Chapin et al., 1986; Meerts, 1997), have slower growth rates (Chapin et al., 1986; Grime, 1977), and that produce less biomass (Grime, 1977). The opposite is true for non-limiting sites. Fertilization can be used as a tool to promote species of better growth rates through increased nutrient supply (Chapin et al., 1986).

Understory vegetation is a major component of the nutrient cycle in conifer stands in the inland Northwest. Understory vegetation increases the total amount of litter added annually to stands and increases total nutrient content in litterfall (Cole et al., 1967; Tappeiner and Alm, 1975; Yarie, 1980; Alaback and Herman, 1988). Species found on infertile sites have lower nutrient concentrations (Chapin et al., 1986; Meerts, 1997), thus the litter has lower nutrient concentrations (Chapin et al., 1986). Over time fertilization may cause a change in species composition (Chapin et al., 1986) that will promote a more productive understory resulting in a greater amount of litter added to a site for decomposition. This will result in conservation of nutrients and a slow release ''fertilization'' over a long period of time after fertilization due to decomposition and a continual cycle of uptake and decomposition (Haines and Haines, 1979; Flanagan and Van Cleve, 1983; Miller et al., 1989; Smethurst and Nambiar, 1989).

Higher nutrient content in the organic matter and an increased amount of organic matter also allows for a larger population of microbes that in turn will increase decomposition rates (Flanagan and Van Cleve, 1983; Chapin et al., 1986; Miller, 1988; Miller et al., 1989). Infertile sites have slower rates of decomposition (Flanagan and Van Cleve, 1983; Chapin et al., 1986) and nutrient release because decomposers are energy limited and plants may contain more phenolics and lignin (Chapin et al., 1986). Therefore, fertilization has the potential to increase nutrient concentrations and increase nutrient turnover rates, altering the nutrient cycle.

Wildlife use understory vegetation in forest stands for a variety of reasons including cover, nesting, and food and many forest stands are also grazed by livestock. The literature summarized above suggests that fertilization can change understory vegetation nutrient concentrations. Nutrient content of forage and browse has a large effect on overall health of both domestic and wild animals, reproductive success, physical

development, and wild animal population size (Shomon et al., 1969; Verme, 1979; Wood, 1986; Holechek et al., 1995). In general, if fertilization increases nutrient concentrations and contents, then all the above animal attributes should increase. Nutrient amounts are highly related to vegetation palatability (Verme, 1979). Palatability increases following fertilization since animals prefer fertilized vegetation to unfertilized (Oh et al., 1970; Anderson et al., 1974; Geist et al., 1974; Verme, 1979; Brockley, 1996; Nams et al., 1996; Kimball et al., 1998).

Fertilization can be used to overcome nutrient depleting factors such as grazing, browsing, and tree harvesting. Naturally, consumption of plants by range animals and wildlife removes nutrients due to animal growth and gaseous products of digestion, and for range animals their eventual removal from the site for slaughter (Dean et al., 1975). Some nutrients are returned through fecal and urine material (Dean et al., 1975) and decomposition of wildlife. However, return of herbivore detritus may occur outside the stand. Therefore, fertilization could be used to increase nutrient amounts and replace nutrients lost to herbivory. Of more significance in terms of nutrient amounts and cycling, whole-tree harvesting can remove large amounts of nutrients from a site and decrease long term productivity (Bigger and Cole, 1983; Tew et al., 1986; Miller et al., 1989). This is mainly due to loss of nutrients in the foliage, crown branches and twigs, and to a lesser extent the bole of the tree and erosion (Tew et al., 1986; Miller et al., 1989; Garrison et al., 2000). Fertilization combined with stem-only harvesting of trees could be used to increase or maintain overstory growth, support grazing, and provide quality wildlife habitat.

There are many environmental variables and species interactions that may not allow for causal effects of fertilization on understory vegetation to be accurately measured. It is important for managers to realize that similar to overstory conifers, each understory vegetation species has different growth rates, nutrient requirements, interactions with other plant species, etc. All the growth and yield models and response studies that we have conducted for conifer species in the Pacific Northwest are miniscule compared to the many studies and models that would need to be developed to explain understory vegetation growth dynamics. Understory vegetation compositions differ based on site quality (Flanagan and Van Cleve, 1983; Chapin et al., 1986; Steele et al., 1981; Johnson and Clausnitzer, 1992), therefore, comparisons between sites can be affected. Age of the overstory species also greatly affects understory composition and nutrient uptake (Turner et al., 1978). This is due not only to limited light (Wellner, 1948; Moir, 1966), moisture (Riegel et al., 1992), and nutrient immobilization within tree biomass as stands develop (Switzer and Nelson, 1972; Garrison and Moore, 1998), but also to different nutrient requirements by the overstory species as they age (Turner et al., 1978; Edmonds et al., 1989; Garrison and Moore, 1998). Chapin et al. (1986) and Edmonds et al. (1989) commented on the fact that fertilization on low fertility sites can lead to rapid uptake by decomposers because they are also nutrient limited. This may have had a small effect on nutrient concentration response from one site to another in this study. Soil moisture amounts can also affect understory uptake of nutrients (Meerts, 1997) and different amounts of precipitation would provide varying amounts of nutrient inputs to the nutrient cycle (Edmonds et al., 1989).

The primary objective of our study was to determine if fertilization changes understory vegetation nutrient concentrations in conifer stands in the inland Northwest. A secondary objective was to determine if fertilization improves wildlife habitat through increases in understory vegetation nutrient concentrations.

2. Methods

2.1. Site description

Four different sites from three general locations, one each in Idaho, Oregon, and Washington were included in this study. These study sites were selected because they are representative of operationally fertilized mid-elevation conifer forests in northeastern Oregon, central Idaho, and central Washington. Elevations ranged between 670 and 1245 m. Precipitation amounts during the sampling period were: Goldendale mixed-conifer site—8.5 cm; New Meadows ponderosa pine site—31.4 cm; both Wallowa sites—30.8 cm (NOAA, 1998). A range of tree densities and overstory species, and both Douglas-fir and grand fir habitat

Table 1
Selected site, stand, and treatment characteristics at the experimental locations

Site	Dominant overstory species	Treat	Initial basal area[a] (m^2/ha)	CCF[a] (%)	Habitat type series[b]	Treatment date	Multi-nutrient fertilizer blend (kg/ha)
Goldendale, WA	Douglas-fir and ponderosa pine	M	15.3	59	Douglas-fir	Spring 1997	B 5.5, Cu 11, K 220, Mo 1, N 220, S 88, Zn 11
		C	14.9	62			
New Meadows, ID	Ponderosa pine	M	17.9	64	Douglas-fir	Fall 1996	B 11, Cu 11, K 220, Mo 1, N 220, S 88, Zn 11
		C	16.3	57			
Wallowa, OR	Mixed-conifer	M	14.4	67	Grand fir	Fall 1995	B 11, Cu 11, K 220, Mo 1, N 220, P 110, S 99, Zn 11
		C	14.2	70			
	Ponderosa pine	M	9.1	34		Fall 1995	B 11, Cu 11, K 220, Mo 1, N 220, P 110, S 99, Zn 11
		C	9.1	34			

[a] Includes all tree species.
[b] After Steele et al. (1981) and Johnson and Clausnitzer (1992).

series were sampled (Table 1). Overstory tree species composition included natural, second-growth, mixed conifers as well as a plantation composed of ponderosa pine. The study sites did not have any sort of overstory tree cutting within the last 10 years. Grazing was excluded from the study sites, except for a light amount at the New Meadows location.

2.2. Study design

The study areas were designed to be fertilizer trials within much larger operational fertilization areas. Size of experimental areas ranged from 10 to 120 ha. The fertilizer and control treatments were randomly assigned to study stands within a site to the extent possible, given operational constraints. Phosphorus was not analyzed because it was only applied at two sites. We assumed that the nutrient did not affect concentrations of other nutrients. Aerial photographs were used to help determine the exact locations of the fertilized units and boundaries were marked for each treatment location. Fertilizers were applied aerially by helicopter and containers were placed throughout each treatment area to collect fertilizer. Collected fertilizer was then weighed to monitor and ensure even distribution throughout the study site. The fertilizer blends and treatment dates for each stand are provided in Table 1.

Understory vegetation for nutrient concentration analyses were mostly obtained from plots developed to measure understory vegetation annual production. Therefore, first, we will briefly describe how overstory vegetation basal area and annual vegetation production was measured, and then describe how nutrient concentrations were obtained in this vegetation. For a greater explanation of how understory vegetation annual production was measured refer to VanderSchaaf (1999) or VanderSchaaf et al. (2002).

One hundred meter transects were established in both control and fertilized areas, with 13 m^2 sub-plots located every 10 m along a transect for a total of 11 sub-plots. The physical arrangement of the various study sites differed resulting in variable number of transects per site. Eight to 10 transects were placed in each stand to minimize variability within a transect as well as capture variation across the treatment unit.

Three life forms were sampled: shrubs, forbs, and grasses and grass-likes (C. geyeri), using the 13 m^2 sub-plots following protocols described in Moeur (1985). The grasses and grass-like life form will further be referred to as grasses. Sampling occurred in mid- and late-summer of 1998. The exact sampling date differed by site to make plant phenological development stage similar between sites. We wanted to sample during the period of maximum understory production and again at the end of the growing season.

Vegetation sampling plots were marked with a PVC pipe in the center. Variable radius overstory tree plots were centered on the vegetation plots to measure overstory tree density and species composition. Each measured tree was marked at diameter breast height (dbh) to assist in future remeasurements. Average basal area per hectare and crown competition factor (CCF) (Krajicek et al., 1961) were calculated as the average of the transects for each treatment (Table 1). Understory vegetation annual production was measured using a modification of the comparative yield method developed by Haydock and Shaw (1975).

At each permanent understory sample plot, two separate components were involved in estimating annual production based on the comparative yield method (Haydock and Shaw, 1975): destructive (clipping and weighing) and non-destructive (ocular estimates) plots. Nutrient concentration analysis was conducted on the vegetation that was clipped during the destructive component. Clipped plots were selected based on the most common species within a site and therefore not all life forms were necessarily represented per site and treatment combination. Additionally, at each 13 m^2 quadrat, the dominant species was recorded based on percent cover measurements (only if at least one species occurred with a minimum of 5% cover). See VanderSchaaf (1999) or VanderSchaaf et al. (2000) for percent cover sampling methodology. The closest plant(s) of this dominant species was located and clipped to obtain a minimum of 2 g green weight. The understory vegetation species analyzed within a life form at both Wallowa sites included the grass *Deschampsia* sp., the forb *Thermopsis* sp., and the shrub *Symphoricarpos albus* (L.) Blake and *Salix scouleriana* Barratt. Understory vegetation analyzed at the Goldendale mixed-conifer site included the grass *Festuca occidentalis* Hook., the forb *Apocynum androsaemifolium* L., the shrubs *Arctostaphylos nevadensis* Gray and *Ceanothus velutinus* Dougl., while the vegetation analyzed at the New Meadows ponderosa pine site included the grass-like *C. geyeri*, the forb *Achillea millefolium* L., and the shrubs *S. albus*, *S. scouleriana*, and *C. velutinus*. Comparisons between multi-nutrient fertilized and non-fertilized individual species were conducted (at least three observations per treatment). *F. occidentalis* and *A. nevadensis* for mid-summer, and *A. androsaemifolium* and *A. nevadensis* for late-summer at the Goldendale mixed-conifer site while at the New Meadows ponderosa pine site, *C. geyeri* for mid-summer and *C. geyeri* and *S. albus* for late-summer were analyzed. No individual species had at least three observations per treatment at the two Wallowa sites. All harvested material was stored in plastic bags, placed in a cooler, transported back to the laboratory, and then oven dried at 78°C for 48 h (Erixson, 1993). Nomenclature follows Hitchcock and Cronquist (1973) for vascular plants studied.

2.3. Chemical analysis

Oven-dried vegetation were ground by life form in a Wiley mill (Intermountain Forest Tree Nutrition Cooperative, 1988). Foliar N concentration was determined using a standard micro-Kjeldahl procedure. Boron, K, molybdenum (Mo), copper (Cu), and zinc (Zn) concentrations were determined by inductively coupled plasma (ICP) emission with digested plant tissue. Both procedures were completed by Scotts Laboratories in Allentown, PA. Sulfur concentration was determined by ICP emission with digested plant tissue. This procedure was conducted at the Holmes Laboratory at the University of Idaho in Moscow, ID.

2.4. Statistical analysis

Concentration of individual nutrients was the dependent variable in our analysis. Nutrient concentrations were computed and analyzed separately for shrubs, forbs, and grasses. Nutrient concentrations were averaged within each site, sampling period, and treatment, and these averaged data were then used in subsequent statistical analyses. The experiment was designed for using analysis of variance (ANOVA), and statistical comparisons between fertilizer treatments were conducted using PROC GLM of the Statistical Analysis System (SAS Institute, 1985). Homogeneity of variance was examined using the Brown–Forsythe test (Brown and Forsythe, 1974), and normality was checked using the Kolmogorov–Smirnov test. For those analyses that did not meet the homogeneity of variance or normality assumptions, logarithmic ($\log_{10}$) transformations were conducted on the dependent variable. These transformed data were then checked to ensure that they met these two assumptions. Simple

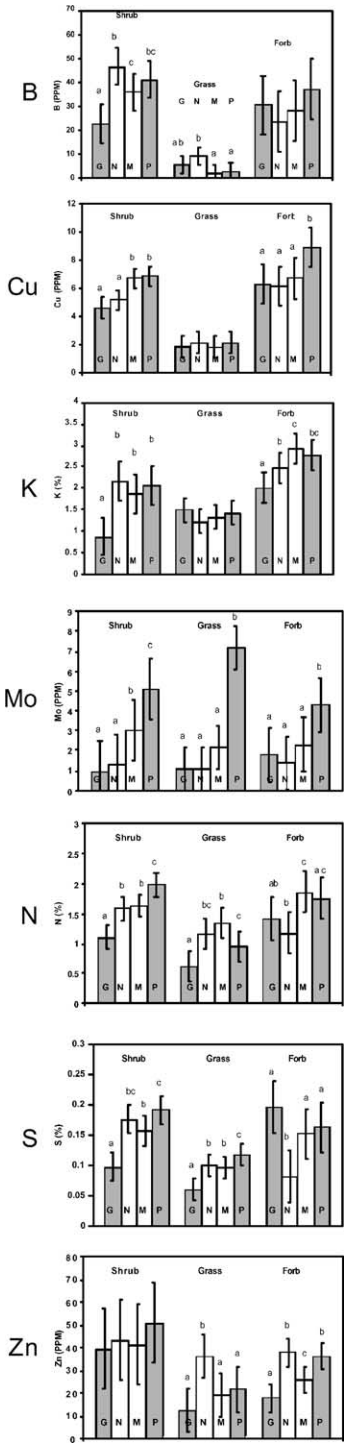

Fig. 1. Concentrations by site for three life forms following operational multi-nutrient fertilization. G: Goldendale, WA

t-tests were conducted for the individual species nutrient concentration analyses. The significance level chosen for all statistical tests was 0.10. Treatment effects were separated using Duncan's multiple range test.

3. Results

For forbs, concentrations differed between sites for Cu, K, Mo, N, S, and Zn (Fig. 1). Excluding statistical differences, most nutrient concentrations were the lowest at the New Meadows ponderosa pine site with the exception of Zn while most nutrient concentrations were the highest at the Wallowa ponderosa pine site. Multi-nutrient fertilization produced differences in concentrations for B, Cu, K, S, and Zn (Table 2).

Concentrations in grasses differed by site for B, Mo, N, S, and Zn. Excluding statistical differences, besides B, Cu, K, and Mo, grasses at the Goldendale mixed-conifer stand had the lowest nutrient concentrations compared to the other three sites. No site consistently had higher nutrient concentrations. Boron, K, Mo, S, and Zn all had changes produced by multi-nutrient fertilization (Table 2).

All nutrient concentrations showed differences between sites for shrubs except for Zn. Excluding statistical differences, all nutrient concentrations for shrubs were the lowest at the Goldendale mixed-conifer site. No site consistently had higher nutrient concentrations. Multi-nutrient fertilization produced differences in B, Mo, N, and S concentrations (Table 2).

Individual species nutrient concentrations showed variability following multi-nutrient fertilization (Tables 3 and 4). Molybdenum significantly decreased but Zn significantly increased in *A. androsaemifolium* during late-summer following multi-nutrient fertilization at the Goldendale mixed-conifer site (Table 3). Significant increases following fertilization were observed for N and S for both sampling periods, K in mid-summer, and B and Cu in late-summer for

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Table 2
Duncans means of nutrient concentrations in three life forms by treatment following multi-nutrient fertilization for four study sites located in the inland Northwest[a]

Nutrient	Shrubs		Grasses		Forbs	
	Control	Multi	Control	Multi	Control	Multi
B (ppm)	31.7a	37.2b	4.8a	7.7b	24.8a	36.5b
Cu (ppm)	5.5a	5.5a	1.5a	2.4a	6.9a	7.5b
K (%)	1.574a	1.642a	1.142a	1.483b	2.379a	2.744b
Mo (ppm)	1.7a	2.3b	1.0a	2.7b	2.3a	3.0a
N (%)	1.405a	1.528b	0.987a	0.951a	1.638a	1.586a
S (%)	0.134a	0.151b	0.079a	0.093b	0.139a	0.171b
Zn (ppm)	40.6a	44.2a	22.4a	26.1b	25.6a	32.4b

[a] Multi—multi-nutrient fertilization; Grasses—grasses and grass-likes (i.e. *C. geyeri*). Means within a life form and nutrient combination that have different letters are significantly different at the 0.10 level.

A. nevadensis. *F. occidentalis* showed significant increases following multi-nutrient fertilization for Cu, K, Mo, and Zn in mid-summer.

At the New Meadows ponderosa pine site, N increased in both *C. geyeri* analyses after multi-nutrient fertilization (Table 4). *C. geyeri* also showed significant increases for K and Mo during mid-summer and B, K, S, and Zn during late-summer following fertilization. No changes in nutrient concentrations were observed for *S. albus* following multi-nutrient fertilization.

3.1. Macronutrient response by individual site, life form, treatment and sampling period combination

Multi-nutrient fertilization showed variable results to change concentrations of macronutrients in understory vegetation (Fig. 2). Grasses showed the most positive response while forbs and shrubs

Table 3
Nutritive concentrations by species following multi-nutrient fertilization at the Goldendale, WA mixed-conifer site for two sampling periods (mid- and late-summer[a])

Nutrient	Species	Mid-summer		Late-summer	
		Control	Multi	Control	Multi
B (ppm)	*A. androsaemifolium*	–	–	21.6a	63.1a
	F. occidentalis	3.4a	8.1a	–	–
	A. nevadensis	21a	24.4a	14.6a	26.4b
Cu (ppm)	*A. androsaemifolium*	–	–	5.7a	6.9a
	F. occidentalis	0.6a	2.7b	–	–
	A. nevadensis	4.3a	4.4a	4.3a	5.0b
K (%)	*A. androsaemifolium*	–	–	1.880a	1.890a
	F. occidentalis	1.318a	1.728b	–	–
	A. nevadensis	0.751a	0.924b	0.842a	0.932a
Mo (ppm)	*A. androsaemifolium*	–	–	3.2a	1.2b
	F. occidentalis	0.6a	1.1b	–	–
	A. nevadensis	0.6a	0.5a	0.9a	0.8a
N (%)	*A. androsaemifolium*	–	–	1.440a	1.580a
	F. occidentalis	0.882a	0.590a	–	–
	A. nevadensis	1.113a	1.290b	0.880a	0.999b
S (%)	*A. androsaemifolium*	–	–	0.213a	0.333a
	F. occidentalis	0.054a	0.058a	–	–
	A. nevadensis	0.079a	0.109b	0.077a	0.091b
Zn (ppm)	*A. androsaemifolium*	–	–	11.1a	16.9b
	F. occidentalis	5.7a	10.5b	–	–
	A. nevadensis	39.7a	35.7a	41.0a	39.2a

[a] Multi—multi-nutrient fertilization. Means within a sampling period, nutrient, and species combination with different letters are significantly different at the 0.10 level.

Table 4
Nutritive concentrations by species following multi-nutrient fertilization at the New Meadows, ID ponderosa pine site for two sampling periods (mid- and late-summer)[a]

Nutrient	Species	Mid-summer		Late-summer	
		Control	Multi	Control	Multi
B (ppm)	C. geyeri	5.6a	8.2a	6.8a	18.2b
	S. albus	–	–	64.6a	64.7a
Cu (ppm)	C. geyeri	2.1a	3.2a	1.9a	2.9a
	S. albus	–	–	4.7a	5.1a
K (%)	C. geyeri	1.200a	1.527b	0.953a	1.497b
	S. albus	–	–	2.783a	2.753a
Mo (ppm)	C. geyeri	0.5a	1.9b	1.2a	1.7a
	S. albus	–	–	2.0a	1.7a
N (%)	C. geyeri	1.049a	1.467b	1.024a	1.500b
	S. albus	–	–	1.160a	1.397a
S (%)	C. geyeri	0.096a	0.117a	0.083a	0.118b
	S. albus	–	–	0.217a	0.153a
Zn (ppm)	C. geyeri	38.0a	47.1a	28.9a	58.8b
	S. albus	–	–	26.5a	30.2a

[a] Multi—multi-nutrient fertilization. Means within a sampling period, nutrient, and species combination with different letters are significantly different at the 0.10 level.

showed more variable response to increased nutrient supplies. There was no change in N concentration across all sites following multi-nutrient fertilization. Potassium concentration in understory vegetation was variable following multi-nutrient fertilization. Increases in K were seen for forbs in late-summer at the Goldendale mixed-conifer site and the Wallowa ponderosa pine plantation, all grass analyses conducted, and shrubs in mid-summer at the Goldendale mixed-conifer site. All other understory vegetation analyses showed no change in K concentration. Sulfur concentration changes showed variable results following multi-nutrient fertilization. Increases in S concentration were seen for forbs in mid-summer at the Wallowa mixed-conifer site, forbs in late-summer at the Wallowa ponderosa pine plantation site, grasses in mid- and late-summer at the New Meadows ponderosa pine site, and shrubs in mid-summer at the Goldendale mixed-conifer site and the mixed-conifer site at Wallowa. All other understory vegetation analyses showed no change in S concentrations.

3.2. Micronutrient response by individual site, life form, treatment and sampling period combination

Multi-nutrient fertilization produced variable changes of micronutrient concentrations in understory vegetation (Fig. 2). Changes in B concentration were variable following multi-nutrient fertilization. Increases in B concentration were seen for forbs in both mid- and late-summer at the mixed-conifer site at Wallowa, grasses in mid- and late-summer at the New Meadows ponderosa pine site, and shrubs in late-summer at the Goldendale mixed-conifer site. All other vegetation analyses showed no change in B concentration. Copper concentration also showed variable results following multi-nutrient fertilization. Increases in Cu concentration were seen for grasses in mid-summer at the Goldendale mixed-conifer site and the New Meadows ponderosa pine site, and shrubs in late-summer at the Goldendale mixed-conifer site. Decreases in Cu concentration were seen for forbs in mid-summer at the Wallowa mixed-conifer site. All other analyses showed no change in Cu concentration. Molybdenum concentration showed variable results following multi-nutrient fertilization. Increases in Mo concentration were seen for forbs in mid-summer at the ponderosa pine plantation at Wallowa and grasses in mid-summer at the Goldendale mixed-conifer site and the New Meadows ponderosa pine site. Decreases in Mo concentration occurred for forbs in both mid- and late-summer at the Goldendale mixed-conifer site. All other analyses showed no change in Mo concentration. Variable results in Zn concentration of understory vegetation were seen following multi-nutrient fertilization. Zinc concentration increased in forbs in mid-summer at the New Meadows ponderosa pine site, forbs in late-summer at the Goldendale mixed-conifer site, and grasses in late-summer at the New Meadows ponderosa pine site. All other analyses showed no change in Zn concentration.

4. Discussion

Multi-nutrient fertilization showed variable results to change macro and micronutrient concentrations in understory vegetation. Similar to Clarks and Haywood (1986), N showed no significant increase following multi-nutrient fertilization in concentration for

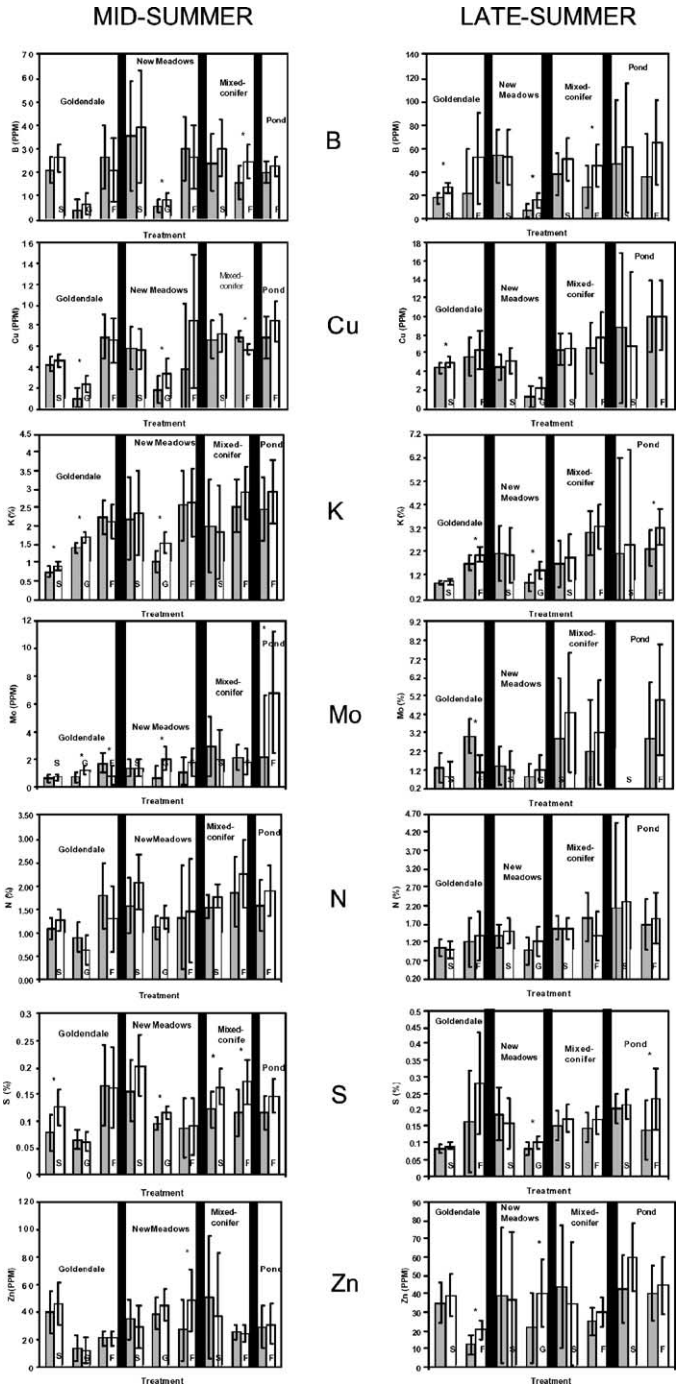

Fig. 2. Concentrations by nutrient and sampling period (mid- and late-summer) for three life forms (S—shrubs, G—grasses and grass-likes, F—forbs) following operational multi-nutrient fertilization. Gray bars are the controls and white bars the multi-nutrient fertilized concentrations. Goldendale: Goldendale, WA mixed-conifer site; New Meadows: New Meadows, ID ponderosa pine site; Mixed-conifer: Wallowa, OR mixed-conifer site; Pond: Wallowa, OR ponderosa pine plantation. An asterisk above a site, sampling period, and nutrient combination indicates the means were significantly different at the 0.10 level. Black bars are used to more clearly separate sites.

herbaceous (grasses and forbs) material (Table 2). One explanation for our results is that N is non-limiting at these sites for the present herbaceous composition. Other studies have found increases in N concentrations in *C. geyeri* following N-only fertilization (Riegel et al., 1991), and in several herbaceous species after N-fertilization in multi-nutrient treatments (Haines and Haines, 1979). Similar to Riegel et al. (1991) we found that *C. geyeri* (Table 4) increased N concentration following multi-nutrient fertilization in both mid- and late-summer. Shrubs showed an increase in N concentration following fertilization across all sites (Table 2); however, no individual site-treatment-sampling period combination showed a significant increase (Fig. 2). At the Goldendale mixed-conifer site *A. nevadensis* showed significant increases in N concentration in both sampling periods (Table 3), but at the New Meadows ponderosa pine site *S. albus* did not have an increase in N concentration (Table 4). Prescott et al. (1993) found that another ericaceous shrub (salal) showed increases following repeated multi-nutrient fertilization treatments. Obviously, different understory species and species compositions require different nutrient amounts (Grime, 1977; Chapin et al., 1986; Meerts, 1997). Current herbaceous vegetation at these study sites, besides *C. geyeri*, may have had adequate N prior to fertilization, such as *A. androsaemifolium* and *F. occidentalis* (Table 3), while shrubs other than *A. nevadensis* may have adequate N prior to fertilization as well. In the future, the fertilization may result in more demanding herbaceous species replacing the present compositions (Chapin et al., 1986).

Overstory nutrient concentration studies were conducted by Shaw (1998) for N at both Wallowa sites. The ponderosa pine plantation overstory showed no difference in N concentration for 1997; however, a significant increase was seen in 1995 and 1996. Nitrogen concentrations at the Wallowa mixed-conifer site did not increase for Douglas-fir during 1995–1997; however, grand fir (Abies grandis (Dougl.) Forbes) showed significant increases for all the 3 years (Shaw, 1998). Therefore, N appeared to be limiting for some of the overstory species. Nitrogen may not have been limiting for the understory vegetation composition present at these sites, or perhaps additional N was not taken up by herbaceous vegetation and most likely shrubs in 1998 because of increased overstory N uptake in the prior years.

Understory vegetation under moderately shade and shade-tolerant overstory species (Wallowa mixed-conifer site) may have limited nutrient access following multi-nutrient fertilization because of greater nutrient demands by these overstory species relative to shade-intolerant overstory species (VanderSchaaf et al., 2002). The Wallowa mixed-conifer site is dominated by grand fir, Douglas-fir, and Engelmann spruce (*Picea engelmannii* Parry). It has been shown that the shade-tolerant grand fir and Engelmann spruce have greater nutrient demands than the moderately shade-tolerant Douglas-fir, and Douglas-fir has greater nutrient demands than the shade-intolerant ponderosa pine (Garrison and Moore, 1998; Garrison et al., 2000). The Goldendale mixed-conifer site is dominated by Douglas-fir and ponderosa pine, while the New Meadows ponderosa pine site is dominated by ponderosa pine. Understory vegetation at these two sites and the Wallowa ponderosa pine plantation may have had more amounts of nutrients available to them following multi-nutrient fertilization due to the overstory species present at these sites. Nutrient concentrations were generally greater for all analyses in the Wallowa ponderosa pine plantation relative to the Wallowa mixed-conifer site, regardless of life form (Fig. 1). This seems to suggest that nutrients may have been more limited to understory vegetation at the Wallowa mixed-conifer site relative to the ponderosa pine plantation. However, other factors may have had an impact as well, when comparing the Wallowa mixed-conifer and ponderosa pine plantation sites. Elevation was similar between the sites (1128 m for the plantation and 1219 m for the mixed-conifer site) but the mixed-conifer site is on a northeast facing slope while the ponderosa pine plantation is on a southeast facing slope. Knoepp and Swank (1997) and Trettin et al. (1999) reported that aspect (e.g. precipitation, soil moisture, and particulate matter) caused differences in nutrient amounts in the soil. The time of the greatest nutrient requirements by overstory trees is close to crown closure (Edmonds et al., 1989; Garrison and Moore, 1998). When the CCF is 100 it is assumed that the site has crown closure (Krajicek et al., 1961). The mixed-conifer site is closer to crown closure (CCFs of 70 (control) and 67 (multi-nutrient fertilized)) while the ponderosa pine

site has less closure (34 for both the control multi-nutrient fertilized). Therefore, the overstory nutrient requirements at the mixed-conifer site may have been greater due to the stage of stand development and not necessarily the tree species. Despite these differences between the sites, the varying overstory species compositions most likely played a role in understory vegetation nutrient concentration and content disparities between sites (Fig. 1).

Although the mixed-conifer site at Wallowa had some nutrient concentration values greater than those at the Goldendale mixed-conifer and New Meadows ponderosa pine sites, other factors are involved. Overstory tree density does not appear to be a factor since all three stands are relatively similar (Table 1). Both the Goldendale and New Meadows sites are Douglas-fir habitat types so these sites are probably less fertile than the Wallowa site. Chapin et al. (1986) and Meerts (1997) state that understory vegetation on infertile sites have lower nutrient concentrations relative to more fertile sites. The Goldendale mixed-conifer site had much less rainfall than all other sites which has been shown to affect nutrient concentrations (Meerts, 1997). Both these phenomena most likely explain why concentrations were generally lower at the Goldendale mixed-conifer site for all shrub and grass analyses (Fig. 1). Our reasoning here is that the lower nutrient concentrations at these two sites relative to the Wallowa mixed-conifer site are due to factors other than the overstory species. If more grand fir and Engelmann spruce were present at the Goldendale mixed-conifer and New Meadows ponderosa pine sites, the nutrient concentrations of the understory would most likely be lower relative to what is now found on the site (assuming that the understory species composition would be constant). It is difficult to make a definitive answer for all understory vegetation species since they have substantial variation in nutrient demand (Grime, 1977; Chapin et al., 1986; Meerts, 1997), and certain understory species may have responded with increased N concentration and others did not on the Wallowa mixed-conifer site. Obviously, this can be said for all other nutrients analyzed in this study as well.

Dilution effects, generally described by Timmer and Stone (1978), are another possible explanation for lack of response in nutrient concentrations in understory species. In order to determine if dilution occurred, nutrient concentrations were averaged across life forms at each site by period and treatment and then multiplied by the estimate of annual production for that site, sampling period, and treatment combination. Estimated contents for all nutrients increased across all sites, life forms, and sampling periods following multi-nutrient fertilization generally by 100% or more except for declines during late-summer at the Wallowa mixed-conifer site. This seems to support our claim that nutrient amounts may be limited for understory vegetation under more shade-tolerant overstory species.

According to our results, K concentration can be increased following application of K in multi-nutrient fertilization operations (Tables 2–4, Fig. 2). However, other studies showed either a variable response in K concentration (Haines and Haines, 1979), no change in K concentration for herbaceous vegetation (Tiarks and Haywood, 1986), or a decrease in K concentration in a shrub (Prescott et al., 1993) when K was applied in fertilizer blends. Contrary to Prescott et al. (1993), we saw a significant increase in K concentration in an ericaceous shrub *A. nevadensis* (Table 3). Increases in K concentration were seen in both mid-summer and late-summer sampling periods (Tables 3 and 4, Fig. 2). Perhaps, K becomes limiting in late-summer for forbs in conifer stands throughout the inland Northwest. All grass analyses showed significant increases in K concentration (Tables 3 and 4, Fig. 2) following multi-nutrient fertilization. Therefore, fertilization may be a means to provide adequate K levels for herbaceous vegetation throughout the entire growing season. For the most part, shrubs did not change in K concentration following fertilization (Tables 3 and 4, Fig. 2), except for at the Goldendale mixed-conifer site (Table 3, Fig. 2). Shrubs, except perhaps *A. nevadensis*, apparently are not limited by K throughout the growing season. Potassium showed no decrease in concentration following fertilization (Tables 3 and 4, Fig. 2).

All life forms showed a significant increase in S and B concentration following fertilization (Table 2). All significant differences in S and B concentrations in understory vegetation by site or individual species were increased (Tables 3 and 4, Fig. 2). Prescott et al. (1993) found that S concentration increased when it was applied in fertilizer blends for a shrub. Increases in S concentration were seen in both