

Response of aboveground biomass increment, growth efficiency, and foliar nutrients to thinning, fertilization, and pruning in young Douglas-fir plantations in the central Oregon Cascades¹

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The effect of thinning and cultural practices (multinutrient fertilization, pruning) on total aboveground biomass increment and growth efficiency was studied over three consecutive 2-year periods (1981–1987) in young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations. Net aboveground biomass increment over the 6-year period averaged 14.5, 7.8, and 5.5 Mg·ha⁻¹·year⁻¹ for the high-, medium-, and low-density plots, respectively. Growth efficiency, after dropping sharply between leaf area indexes of 1 and 6 m²/m², remained relatively constant up to a leaf area index of 17, the highest measured. Consequently, aboveground biomass increment continued to increase at leaf area indexes well above that at which the Beer-Lambert law predicts maximum light should be absorbed. Foliage analyses indicate that thinning improved nitrogen, potassium, and magnesium nutrition and increased the translocation of potassium from 1-year-old foliage to support new growth. However, fertilization increased foliar nitrogen and phosphorus contents only when coupled with pruning, suggesting that trees favor total leaf area over individual needle nutrition. Indications of potassium and magnesium limitations in this study are supported by other recent studies in Douglas-fir. Further work on the role of multinutrient deficiencies in this species is warranted.

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L'effet de l'éclaircie et de pratiques culturales, comme la fertilisation avec plusieurs éléments nutritifs et l'élagage, sur l'accroissement de la biomasse aérienne totale et sur la capacité de croissance a été étudié pendant trois périodes de 2 années consécutives, de 1981 à 1987, dans de jeunes plantations de Douglas taxifolié (*Pseudotsuga menziesii* (Mirb.) Franco). L'accroissement net de biomasse aérienne pour la période de 6 ans était en moyenne de 14,5, 7,8 et 5,5 Mg·ha⁻¹·an⁻¹ respectivement, pour les parcelles de densité élevée, moyenne et faible. Après une diminution abrupte pour des indices de superficie foliaire allant de 1 à 6 m²/m², la capacité de croissance est demeurée relativement constante jusqu'à un indice de superficie foliaire de 17, la valeur la plus élevée. Par conséquent, l'accroissement de la biomasse aérienne a continué d'augmenter pour des indices de superficie foliaire dépassant nettement ceux pour lesquels de maximum d'absorption lumineuse est atteint selon la loi de Beer-Lambert. Les analyses foliaires indiquent que l'éclaircie a amélioré la nutrition en azote, en potassium et en magnésium et a augmenté la translocation de potassium en provenance du vieux feuillage pour supporter la nouvelle croissance. Cependant, la fertilisation a augmenté le contenu foliaire en azote et phosphore seulement lorsqu'elle était couplée à l'élagage, suggérant que les arbres favorisent la superficie foliaire totale plutôt que la nutrition d'aiguilles individuelles. L'observation de déficiences en potassium et magnésium observés dans cette étude est supportée par d'autres études récentes sur le Douglas taxifolié. D'autres travaux sur le rôle des déficiences multiples chez cette espèce sont nécessaires.

[Traduit par la rédaction]

Introduction

Understanding the factors that control forest productivity, and how these are influenced by cultural treatments, has always been a central goal of forestry research. This understanding is even more important now, as foresters increasingly attempt to balance wood production with maintaining biological diversity and long-term site productivity. In this phase of a larger study, we estimated total aboveground biomass increment and growth efficiency (GE; aboveground biomass increment per unit of leaf area (Waring 1983)) and determined foliar nutrient levels in four Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations that had received various treatment combinations of thinning and cultural practices (multinutrient fertilization and pruning). GE incorpo-

rates the influences of both photosynthetic efficiency and carbon allocation to aboveground tissues (Vose and Allen 1988) and can serve as an index of general stand vigor or disease resistance (Waring and Pitman 1985).

Growth response to thinning and fertilization has received a great deal of attention in forestry. Studies of Douglas-fir include those of Brix (1981, 1983), Binkley and Reid (1984), Barclay and Brix (1985), and Barclay *et al.* (1986). Most work on tree nutrition has focused on growth response to nitrogen (N) fertilization, with the result that relatively little is known about the degree to which nutrients other than N may limit productivity. Recently, however, researchers have utilized foliar nutrient concentration and contents to explore the influence of multiple nutrients on growth (Weetman and Algar 1974; Timmer and Stone 1978; Morrow and Timmer 1981; Timmer and Morrow 1984; Pang *et al.* 1987). So far as we know, ours is the first experiment in coniferous forests to investigate the effects of multiple nutrient fertilization over a range of stand leaf area indexes (LAIs).

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TABLE 1. Topoedaphic variables for the four Douglas-fir plantations studied, Western Hemlock Zone, Oregon Cascades

Site	Mean elevation (m)	Soil rock content (%)		Slope (%)		Aspect (degrees)	
		Mean	Range	Mean	Range	Mean	Range
L107	705	11.2	5.2–18.3	41	12–75	168	0–360
L111	732	8.4	2.7–20.5	43	25–65	277	200–360
L405	854	6.6	1.9–15.7	23	12–50	182	155–215
L701	854	14.6	7.6–27.0	42	12–63	166	100–252

TABLE 2. Estimated fertilizer additions, by density level, to the four Douglas-fir plantations

Nutrient	Density level		
	Low	Medium	High
Nitrogen			
kg/ha	31.0	51.0	163.0
g/tree	94	89	51
Phosphorus			
kg/ha	6.9	11.1	35.6
g/tree	21	19	11
Potassium			
kg/ha	6.2	10.1	32.3
g/tree	19	18	10
Calcium			
kg/ha	4.1	6.7	21.4
g/tree	12	12	7
Sulfur			
kg/ha	2.5	4.1	13.2
g/tree	8	7	4
Iron			
kg/ha	0.5	0.3	2.7
g/tree	2	1	1

Pruning, widely used in some areas to improve wood quality in plantations with widely spaced trees (e.g., Evans 1982), is gaining favor in the Douglas-fir region. However, effects of pruning on tree and stand growth are unclear. Reducing leaf area probably lowers individual tree growth to some degree, and also stand growth if LAI drops too low (Jarvis and Leverenz 1983). But growth losses would be mitigated somewhat if GE of pruned trees increased, something that is likely if pruning removes older branches with a relatively high ratio of respiring tissues (wood) to photosynthesizing tissues (leaves). GE would also be increased if pruning improved the nutrition or water relations of residual leaves (e.g., Fife and Nambiar 1984).

Our objectives in the research reported herein were to (i) study the interacting effects of nutrient availability and stand leaf area on aboveground biomass increment and GE of Douglas-fir and (ii) examine foliar nutrient status and changes in needle weight as a result of thinning and cultural practices.

Study site

The study was undertaken on the H.J. Andrews Experimental Forest, located about 80 km east of Eugene, Oregon, in the Blue River Ranger District, Willamette National Forest (44°15'N, 122°10'W).

The climate of the experimental forest is wet and fairly mild in winter and warm and dry in summer (Bierlmaier and McKee 1989). Yearly average daily air temperature is 8.5°C. At low elevation, the January mean temperature is 2.3°C and the July mean is 26.6°C (Rothacher *et al.* 1967). Extreme temperatures range from about -18 to 38°C. Annual precipitation, about 80% of which falls in winter, averages about 2300 mm at lower elevations and may exceed 2500 mm on some higher ridges (Dyrness *et al.* 1974).

Most soils of the experimental forest are classified as Inceptisols, but some Alfisols are present (Brown and Parson 1973). The highly porous soils allow rapid absorption of water and provide storage for 30–40 cm of water (Bierlmaier and McKee 1989).

Vegetation of the experimental forest, typical of the central portion of the western slope of the Oregon Cascade Range, is stratified into two major forest zones: the Western Hemlock (*Tsuga heterophylla*) Zone, generally below 1050 m and with abundant western hemlock and Douglas-fir; and the Pacific Silver Fir (*Abies amabilis*) Zone, generally above 1050 m and with abundant Pacific silver fir (Bierlmaier and McKee 1989).

Our study plots were installed in four Douglas-fir plantations, all in the Western Hemlock Zone of Franklin and Dyrness (1973). Topoedaphic characteristics of the study sites are provided in Table 1. The plantations ranged in age from 21 to 27 years (dated from planting) in 1987, and had been established with 2-0 Douglas-fir following clear-cutting and slashburning.

Methods

Treatments

The experimental design was a split plot with three density levels as main plots and four cultural practices as subplots. Each of the four plantations served as a block, giving 48 subplots in total. Plantations were selected to represent a range of elevations and topographies. Although this increases experimental error because of uncontrolled environmental variation among blocks, it widens the study's scope of inference.

In 1981, the plantations were heavily thinned (to low-density level: average, 300 trees/ha), moderately thinned (to medium-density level: average, 604 trees/ha), or unthinned (high-density level: average, 3459 trees/ha). Within a plantation, each density level (low, medium, high) was represented by one randomly selected main plot, which was further divided into four subplots separated from one another by a 10-m buffer strip. Each subplot contained 35–50 trees regardless of density level, and hence varied in area depending on stocking. A cultural practice (pruning, fertilization, pruning and fertilization combined) was randomly applied to one subplot per main plot in 1982 and again in 1984. In addition, one subplot per main plot was neither pruned nor fertilized.

Trees were pruned with a standard pruning saw attached to a 2.5 m long handle. The percentage of crown removed varied with tree size relative to the average tree size within a given subplot; dominants were pruned most heavily, and small intermediates were pruned lightly or not at all. Trees of average DBH and larger on a given subplot had from 20% to a maximum of 40% of their crown removed; trees smaller than average had from 0 to 15%. This protocol was not

TABLE 4. Estimated stocking, leaf area index (LAI), and aboveground biomass accumulation, by density level, in the four Douglas-fir plantations (standard error of the means is in parentheses)

Variable, by density level	Measurement year			
	1981	1983	1985	1987
No. of trees/ha				
High	3459	3432	3305	3201
Medium	604	600	593	587
Low	300	299	298	295
LAI (m ² /m ²)				
High	—	7.9 (0.89)	9.3 (0.96)	10.7 (1.0)
Medium	—	3.0 (0.23)	3.7 (0.25)	4.4 (0.26)
Low	—	1.8 (0.10)	2.3 (0.12)	2.8 (0.15)
Biomass (Mg/ha)				
High	86.1 (13)	115.7 (15)	142.8 (17)	173.3 (18)
Medium	34.7 (4.7)	49.7 (5.9)	64.8 (6.0)	81.8 (7.5)
Low	18.9 (1.4)	29.1 (1.9)	34.8 (2.5)	52.2 (3.0)

biomass, expressed as milligrams per 10 needles, was obtained by weighing five lots of 10 randomly selected needles per subplot from the dried foliage used for nutrient analyses.

Potassium, C, and magnesium (mg) concentrations were determined by perchloric acid digestion. Twelve milliliters of concentrated HNO₃ were added to 1 g of foliage in a flask and boiled. Then flasks were cooled and 6 mL of perchloric acid was added; flasks were again heated and samples digested for about 20 min. Samples were removed from the hot plate and cooled 1–2 min; 15 mL of deionized water was added and filtered immediately through Whatman No. 50 filter paper into 100-mL volumetric flasks. Volumetric flasks were brought to volume with deionized water. Samples were analyzed with an atomic absorption spectrophotometer.

Nitrogen and P concentrations were determined by micro-Kjeldahl digestion. A 0.5-g foliage sample was placed in a 75-mL digestion flask, to which 2.2 g of catalyst mix (100 parts K₂SO₄, 10 parts CuSO₄·5H₂O, and 1 part Se), 10 mL of H₂SO₄, and 4–6 mL of 30% H₂O₂ were added. Samples were digested for approximately 3 h, removed from the digestion unit, and cooled. Distilled water was added to the flasks, which then were shaken three times. Finally, a 3.5-mL aliquot was analyzed for N and P in an Alpken Rapid Flow Analyzer (R.F.A-300).³

Statistical analysis

Analyses of variance (ANOVA) and Tukey's test were used to investigate treatment differences, which were screened at the 0.05 level (Steel and Torrie 1980). Data were log transformed to achieve a normal distribution.

Results

Aboveground biomass increment

The ANOVA of aboveground biomass increment (per hectare) showed a highly significant density effect in all measurement periods and an increasingly significant effect of cultural practices in each period, but no significant interaction between density level and cultural practices (Table 3). Sites did not differ. Net aboveground biomass increment over the 6 years averaged 14.5, 7.8, and 5.5 Mg·ha⁻¹·year⁻¹ in the high-, medium-, and low-density plots, respectively (Fig. 1a). Productivity remained relatively constant throughout the entire period within a given density level. In 1987, above-

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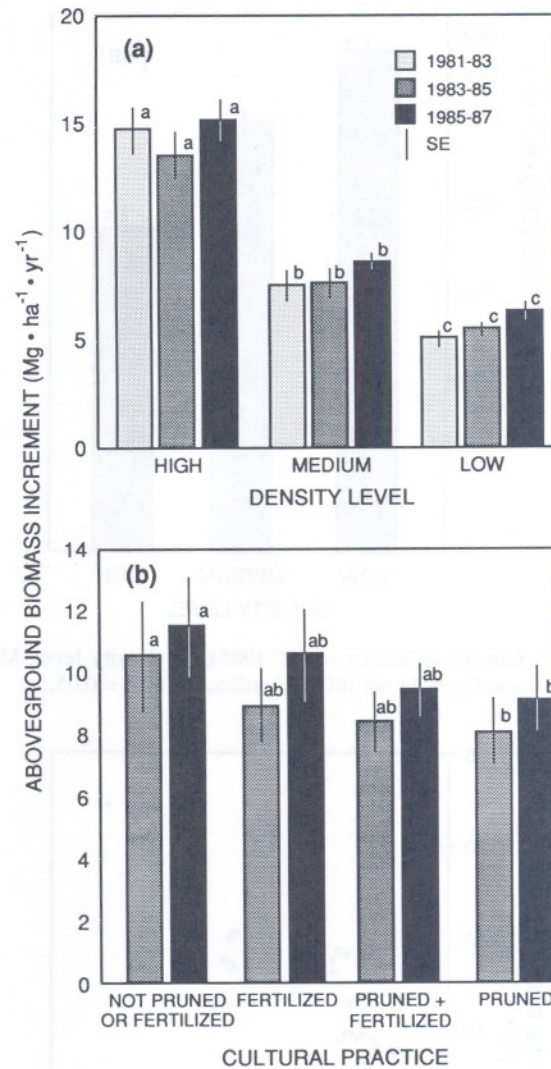


FIG. 1. Total aboveground biomass increment by (a) density level (over three measurement periods) and (b) cultural practice (over two measurement periods). Means with the same letter do not differ significantly at $P = 0.05$.

ground tree biomass averaged roughly 173, 82, and 52 Mg/ha in the high-, medium-, and low-density plots, respectively, having increased 100, 135, and 176% between 1981 and 1987 (Table 4). Expansion of LAI between 1983 and 1987 was also greatest at high densities and least at low densities (Table 4). In 1987, LAI averaged 10.7, 4.4, and 2.8 m²/m² in high-, medium-, and low-density plots, respectively.

Significant effects of cultural practices during the 1983–1985 and 1985–1987 periods were due to less growth in the pruned and the pruned and fertilized subplots than in the subplots that were neither pruned nor fertilized (Fig. 1b).

Growth efficiency

Density level had the largest effect on GE in both the 1983–1985 and 1985–1987 measurement periods (Table 3). GE during 1983–1985 averaged 188, 248, and 290 g·m⁻²·year⁻¹ in the high-, medium-, and low-density plots, respectively (Fig. 2), whereas GE during 1985–1987 averaged 180, 236, and 268 g·m⁻²·year⁻¹ for the same density levels. Although aboveground biomass increment during

TABLE 5. Mean values (with standard errors in parentheses) for nutrient composition and needle weight of 1-year-old and current Douglas-fir foliage for different density levels

Foliage age, by density level	Nutrient concentration (%)					Nutrient content ($\mu\text{g}/10$ needles)					Needle weight (mg/10 needles)
	N	P	K	Ca	Mg	N	P	K	Ca	Mg	
One year old (1987)											
High	0.96 _b	0.27 _a	0.66 _a	0.94 _a	0.14 _a	408 _b	113 _a	273 _{ab}	406 _a	58 _a	42 _b
Medium	1.07 _a	0.24 _a	0.63 _a	0.88 _a	0.13 _a	450 _b	102 _a	266 _b	369 _a	55 _a	42 _b
Low	1.09 _a	0.24 _a	0.63 _a	0.86 _a	0.12 _a	520 _a	115 _a	301 _a	410 _a	60 _a	47 _a
	(0.074)	(0.016)	(0.015)	(0.042)	(0.005)	(56.6)	(7.0)	(18.7)	(22.2)	(2.5)	(3.0)
Current (1988)											
High	1.01 _b	0.25 _a	0.86 _a	0.66 _a	0.13 _a	365 _b	84 _b	299 _b	221 _a	43 _b	35 _b
Medium	1.09 _a	0.21 _b	0.93 _a	0.59 _a	0.13 _a	416 _b	81 _b	348 _{ab}	218 _a	48 _{ab}	38 _b
Low	1.15 _a	0.21 _b	0.83 _a	0.55 _a	0.11 _a	534 _a	98 _a	378 _a	254 _a	53 _a	46 _a
	(0.070)	(0.019)	(0.052)	(0.057)	(0.007)	(86.8)	(9.35)	(40.1)	(20.0)	(4.81)	(5.8)

NOTE: Within a column in the same year, means followed by the same letter do not differ significantly ($P < 0.05$, Tukey's test).

by Weetman (1971) and Timmer and Stone (1978). Although this technique was designed to evaluate fertilizer responses, it has also been used successfully to assess response to other silvicultural treatments such as thinning (Timmer and Morrow 1984). Graphical analyses of current foliage on our trees indicate that N, K, and Mg nutrition was improved by thinning, N sustaining the strongest and most statistically significant effects (Fig. 5). We can see from the graphs that the greater weight of needles on low- than high-density plots was accompanied by either unchanged or higher concentrations of N, K, and Mg, indicating that heavy thinning improved foliar nutrition of those elements (refer to Table 5 for the probability levels). In contrast, the concentration of P in current foliage drops as needle weight increases (i.e., is lower on low- than high-density plots), indicating that the supply of that element was sufficient at high stocking densities to meet the demands of current foliage. Binkley (1986) discusses the rationale behind these interpretations.

As with current foliage, 1-year-old needles were significantly heavier in the low- than in the high-density plots and had greater N content (Table 5, Fig. 5). Potassium content averaged higher in the low- than high-density plots, but the difference was small and not significant at $P = 0.05$. Content of other nutrients in the 1-year-old foliage did not differ between low and high densities.

Patterns were somewhat different in the 1-year-old foliage of the medium-density plots. Needle weights did not differ from those of the high-density plots; however, both N concentration and content were higher. Increased N content with no concomitant increase in needle weight may indicate that some other factor limited needle growth, or alternatively that less N was translocated from 1-year-old needles in the medium- than high-density plots. In contrast, both concentration and content of other nutrients in 1-year-old needles averaged lower in the medium- than in the high-density plots. Differences were not statistically significant; however, the consistency of the response among the different nutrients suggests that the differences may be real.

Comparing 1-year-old and current foliage from trees growing at the same density level gives some indication of differences among those levels in nutrient translocation. Potassium content of 1-year-old foliage averaged 9, 24, and 20% lower than that of current foliage in the high-, medium-,

and low-density plots, respectively, suggesting greater translocation in the thinned than in the unthinned plots (Table 5). Nitrogen concentration averaged higher in current than 1-year-old foliage at all density levels, but because current foliage weighed less than 1-year-old foliage, this translated into higher average N content only in the low-density plots, and even this difference was quite small. Content of other nutrients either did not differ by foliage age or was higher in the older needles.

Effects of cultural practices

Within a given density level, differences in needle weight among the cultural practices were small and statistically insignificant at $P = 0.05$ (Table 6; data for medium density not shown).

Fertilizing the high-density plots raised current foliar content of N, K, P, and Mg, but except for K, this occurred only when fertilization was coupled with pruning (Fig. 6). In the case of Ca and P, fertilization without pruning resulted in rather sharp declines in both concentration and content in current foliage. Fertilization both with and without pruning lowered content of all nutrients except Ca in 1-year-old foliage (Fig. 6), suggesting increased translocation to support new growth. That nutrient declines do reflect translocation is supported by the fact that Ca, generally considered immobile in plant tissues, was the only nutrient whose content did not decline in the older needles.

At low density, several nutrients responded positively to one or more treatments. Potassium content of 1-year-old foliage averaged nearly 25% higher in fertilized and 10% higher in pruned and fertilized trees than in controls (Fig. 7). Changes in foliar nutrient content of other elements in fertilized, low-density plots varied depending on whether or not trees were also pruned; as in high-density plots, nutrient status was consistently better in pruned and fertilized trees. Fertilization without pruning resulted in rather sharp drops in concentration and content of Ca and Mg in 1-year-old foliage, and of N, P, and Mg in current foliage (Fig. 7). In current foliage, all nutrients but Ca behaved similarly when trees were pruned or pruned and fertilized, their responses indicating relief of deficiency when pruned, and luxury consumption when pruned and fertilized. Such patterns probably reflect competition for

TABLE 6. Mean weight (with standard errors in parentheses) of 1-year-old and current Douglas-fir needles for different cultural practices at different density levels (no values differ significantly ($P < 0.05$, Tukey's test))

Foliage age, by cultural practice	Weight (mg/10 needles), by density level	
	High	Low
One year old (1987)		
Pruning	40.9	48.5
Fertilization	43.7	47.1
Pruning and fertilization	41.5	48.5
No pruning or fertilization	42.9 (1.35)	45.7 (1.35)
Current (1988)		
Pruning	31.5	49.6
Fertilization	35.6	41.8
Pruning and fertilization	39.4	45.8
No pruning or fertilization	32.9 (0.64)	47.1 (0.64)

on data of Ingestad (1979), gives the optimum ratios of K and Mg to N in Douglas-fir foliage as 0.5 and 0.04, respectively; however, our trees never dropped below a K/N ratio of 0.7 and an Mg/N ratio of 0.1. These discrepancies may reflect differences between the nutrient requirements of 25-year-old trees in the field and those of seedlings used to derive optimum nutrient levels, or differences in where needles were sampled within crowns (our samples were midcrown). More in line with our findings, van den Driessche (1979) gives 0.8% as a "marginal" foliar K concentration for Douglas-fir growing on the western slope of the Cascades. Douglas-fir in the Intermountain Region of the western United States does not respond to N fertilization when K/N ratios are below 0.65 (Mika and Moore 1990).

Nutrient limitation at high LAI is supported by the fact that GE was significantly higher in fertilized than in neither pruned nor fertilized subplots at high-density levels. Fertilization alone did increase foliar K content in the high-density plots, but foliar N and P content were increased only when fertilization was coupled with pruning (Mg was not contained in the fertilizer tabs). The latter finding is consistent with that of Fife and Nambiar (1984) in radiata pine (*Pinus radiata* D. Don). Apparently, competition for nutrients within the crowns of individual trees acts to maintain high leaf biomass at the expense of needle nutrition, a response that should tend to decrease rather than increase GE. That fertilization alone improved GE in the high-density plots might be attributed to improved K nutrition, or perhaps to S or Fe, which were added in the tabs but not measured in the foliage. Both S and Fe limitations have been previously reported for Douglas-fir (Turner *et al.* 1977; Perry *et al.* 1984; Edmonds and Hsiang 1987).

The ratio of Ca to other nutrients in foliage was sharply lower in the fertilized than in the unfertilized trees, suggesting less structural tissue in the former. Therefore, improved GE in the fertilized plots may have resulted from changes in needle physiology not readily apparent from the measures we made. Multiple regression shows that of all our measures of foliar and soil nutrients, GE in the high- and medium-density plots correlates most strongly with anaerobic mineralizable N

(N_{min} ; A. Velazquez-Martinez and D.A. Perry, in preparation). That does not necessarily implicate N as the cause of improved GE, however. In fact, the simple correlation between N_{min} and foliar N is insignificant ($P = 0.05$) at all density levels (A. Velazquez-Martinez and D.A. Perry, in preparation). N_{min} correlates strongly with total microbial biomass as measured by the standard fumigation technique (Myrold 1987; S. Hart and T.E. Bell, unpublished data), and hence reflects numerous soil processes that might influence tree growth. The increase in foliar Mg content with fertilization and pruning (although Mg was not contained in fertilizer tabs) suggests that fertilization enhanced root and mycorrhiza activity, and thus the ability of trees to gather water and nutrients.

Nitrogen, long considered the most limiting nutrient in Douglas-fir forests, did show the strongest foliar response to thinning in this study. Our findings with Mg and K were unexpected, but are supported by other recent studies. Potassium has been found to limit Douglas-fir response to N fertilization in the Intermountain Region (Mika and Moore 1990), and there is evidence for Mg limitations in Douglas-fir growing elsewhere in western Oregon (N. Vance, personal communication). Foliar Mg content explains 49% of the variation in relative LAI increment (leaf biomass increment per unit of leaf biomass) in our low-density plots, whereas foliar K content explains 45% of the variation in relative LAI increment in our medium-density plots (A. Velazquez-Martinez and D.A. Perry, in preparation). These patterns are especially surprising because the andesitic soils of the Cascades are not particularly acidic and have higher levels of exchangeable cations than many forest soils.

Comparing K content of current and 1-year-old foliage suggests that considerably more of this element is translocated from older foliage to new growing points in thinned than in unthinned plots. Others have reported increased nutrient translocation with improved growing conditions in conifers. Nambiar and Fife (1987) found that N fertilization resulted in greater translocation of N, P, and K from older foliage of radiata pine, and Oren *et al.* (1988) showed that N fertilization from acid precipitation induces greater Mg translocation from old foliage of Norway spruce (*Picea abies* (L.) Karst.). Chapin and Kedrowski (1983) also suggest that improved tree nutrition results in more nutrients being translocated from old foliage to new growing points.

The fact that twigs grow faster and reach a larger final size when exposed to more light (Oren and Schulze 1989) may account for much of the relatively high K translocation in our thinned plots. However, the improved N supply in thinned plots may have also induced greater translocation of K from 1-year-old foliage (Oren *et al.* 1988; Oren and Schulze 1989). The lower average content of all nutrients except N in 1-year-old foliage of the medium- compared with the high-density plots raises the possibility that N may have been relatively more available than the other nutrients after moderate thinning. More sampling will be needed to test the validity of this, however.

Effects of cultural practices were quite different in the low- than in the high-density plots, fertilization in particular reducing average current needle weight and content of N, Ca, and P. Except for Ca, these declines did not occur in trees that had been pruned. Foliage for nutrient and weight measurements was collected from midcrown branches, whereas lower branches were pruned, suggesting that the unshaded

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these vary with soils and other environmental factors. The experimental approach used here, multinutrient fertilization coupled with foliage analyses, shows promise as a relatively efficient field technique for identifying patterns of nutrient deficiency that can then be tested more rigorously in a traditional factorial experiment.

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