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The response of light, water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir forests

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ABSTRACT

Fire suppression and limited forest management have caused overstocking in many forests across the western United States. Overstocked stands have higher competition for limiting resources and causes tree stress. The amount of stress a tree experiences is related to the current availability of resources (site productivity), and the competition for those resources (stand density). Stressed trees are more susceptible to insects, disease, and mortality, which cause fuel buildup and increase wildfire risk. Pre-commercial thinning (PCT) can alleviate stress by decreasing the amount of competition in younger stands. The objective of this study was to determine how reducing competition through PCT might improve resource availability to trees at a range of initial stand conditions.

We used a triplet-plot approach including 4.3 m and 5.5 m spacing and compared those to unthinned controls in stands varying in site productivity (height growth) and density (initial stand basal area) throughout northern Idaho and northeastern Washington. Stands were dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Douglas ex D. Don) Lindley), and western red cedar (*Thuja plicata* Donn ex D. Don). As expected, higher density stands intercepted greater amounts of light. Thinned stands intercepted 33–58% less light than controls, depending on tree spacing. Site productivity was positively correlated with soil moisture in the spring and soil temperature in both the spring and summer. Pre-commercial thinning increased soil moisture by 6% in the spring and 10% in the summer, and soil temperature increased by 0.5 °C in spring and 1 °C in summer. Douglas-fir foliar N, Ca, Zn concentration decreased after thinning, while P and B increased and S, K, and Cu were unchanged. Thinning had the greatest relative impact on summer soil moisture, followed by soil N availability, and light interception. Thinning response studies frequently focus on light availability; our results demonstrate that the response of soil moisture and nutrient availability exceeded that of light availability for the studied forest types.

1. Introduction

Fire suppression and lack of adequate density management in the Pacific Northwest cause many forest stands to be overstocked. Overstocked stands experience greater competition for growth-limiting resources, including light, water, and nutrients, causing tree stress within the stand (Cole and Newton, 1986; Nambiar and Sands, 1993). In addition to greater competition, changing climatic conditions are putting further stress on trees (Chmura et al., 2011; Elkin et al., 2015). Stress reduces the ability of trees to resist insects and disease and increases the likelihood of mortality (Stoszek et al., 1981; Louda and Collinge, 1992). Overstocking and greater amounts of mortality lead to fuel buildup, creating higher wildfire hazard (Schoennagel et al., 2004). Thus, understanding or estimating the amount of stress or competition a tree is experiencing is critical for prioritizing forest management decisions.

How much stress a tree experiences is largely a function of the availability of the resources essential for tree growth and development (light, water, nutrients), and the amount of competition for those resources (Dobbertin, 2005; He and Duncan, 2000). However, it is easier to measure and quantify the forest growth or productivity than it is to directly measure resource availability. A common indirect measure for the availability of resources or "site quality" at a location is forest productivity or site index. Site index is commonly expressed as the amount of height growth over a given amount of time for the largest or "dominant" trees of a certain species (Monserud, 1984). Higher site index at one location indicates better site quality than lower site index at a different location.

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How resource availability changes with differences in site quality is largely unknown, thus making site quality manipulations difficult and costly. Consequently, forest managers commonly focus efforts on decreasing competition for limiting resources by lowering stand density.

Forest stand density characterizes the amount of competition among trees. The most common metrics of density combine the number of trees per area, and the size of those trees (Reineke, 1933; Curtis, 1982). Higher densities suggest greater competition for resources and therefore, more stress. Suppressed trees, or those with the least competitive advantage, suffer the highest stress levels and will likely die without relief from competition (Dobbertin, 2005). Lowering stand density by removing trees will decrease competition, relieve stress, and improve forest resource availability. Lower competition after thinning also provides residual trees a better chance to cope with changing climatic conditions (Chmura et al., 2011; Giuggiola et al., 2013; Sohn et al., 2013). A common silvicultural practice that reduces the density of forests is pre-commercial thinning.

Pre-commercial thinning (PCT) reduces the density of a forest by felling undesirable trees at a young age to achieve a preferred species composition and spacing. Lower competition resulting from thinning allows for better crown development and growth of residual or "crop" trees (Ferguson et al., 2011), decreased rotation lengths, and better product dimensions (Curtis, 2006). Thinning also increases crop tree resistance to insect attack (Waring and Pitman, 1985) and can decrease the risk of wildfire (Moghaddas and Stephens, 2007). The amount of competition or stress relief depends on both pre- and post-thinning stand conditions. After thinning, limiting resources become more available for both forest and tree growth because of lower competition (Thibodeau et al., 2000; Sterba, 1988).

Resources that initially respond to PCT are either physical resources, such as light, water, and temperature, or chemical resources, such as soil nutrients. Such resources are available immediately after thinning, and continue to respond dynamically as the trees reoccupy the available growing space. More light penetrates tree crowns after PCT, which results in greater photosynthetic capacity for the residual trees (Brockley, 2005; Ferguson et al., 2011). Soil moisture increases after PCT by greater throughfall, less stand water use, and decreased evaporation from higher slash loads (Stogsdill et al., 1992; Smethurst and Nambiar, 1990). Higher soil and pre-dawn shoot water potentials indicate lower post-thinning water stress (Brix and Mitchell, 1986; Laurent et al., 2003). Reduced tree water stress by thinning is a viable option for improving forest resiliency to drought induced by climate change (D'Amato et al., 2013; Elkin et al., 2015; Sohn et al., 2013). Soil temperatures after thinning increase by as much as 2 °C (Thibodeau et al., 2000), which provides a more suitable environment for soil biota and nutrient mineralization processes (Powers, 1990).

Chemical or nutrient resources also respond to PCT and are just as important for tree growth as physical resources. Yet the thinning response to nutrients is not well understood because it is difficult to monitor changes in nutrient availability over time given the high spatial variation that is commonly observed (Binkley, 1986). Nutrient limitations are common in forest ecosystems (Bergh et al., 1999; Davidson et al., 2004; Valentine and Allen, 1990; Webster and Dobkowski, 1983). Foliar nitrogen (N) is commonly beneath critical levels for Douglas-fir, ponderosa pine, and grand fir within the Inland Pacific Northwest of the United States (Moore et al., 2004). Additional nutrient deficiencies in sulfur (S), potassium (K), and boron (B) are often regionally found in Douglas-fir foliage (Coleman et al., 2014). Thinning may alleviate competition for these limiting nutrients. A majority of the nutrients acquired by trees reside in the foliage (Garrison and Moore, 1998), which PCT operations leave on site. Nutrients and organic matter from trees felled after PCT incorporate into the soils, providing greater availability of nutrients to residual trees (Sterba, 1988). Increased foliar N, phosphorous (P), and K concentrations occur after PCT (Carlyle, 1995; Thibodeau et al., 2000), although these results are not consistent across species and regions (Ginn et al., 1991; Velazquez-Martinez et al., 1992). Changes in foliar nutrient concentration dissipate as the canopy responds to changes in nutrient availability (Hokka et al., 1996; Gower et al., 1992). The dynamic nature of nutrient pools and their relationships with other resources (water, temperature) make them difficult to measure (Sands and Mulligan, 1990). Furthermore, how well residual trees are able to acquire these nutrients is uncertain. There is little information about how resources respond to thinning at various initial site conditions. The objective of this experiment was to determine how reducing competition through PCT affected relative resource availability at a range of site productivity and initial stand density with respect to tree and stand growth response.

2. Material and methods

2.1. Study design

We selected 14 sites across northern Idaho and northeastern Washington to represent the range of forest site productivity and stand density commonly found across the region (Fig. 1). Site productivity was determined by measuring dominant Douglas-fir height growth for the last 10 distinct growth whorls (Table 1). If 10 whorls were not well distinguished, height growth for the last five whorls was measured and doubled for comparing to 10-year growth measurements. All measurements were taken after thinning treatments were established. Therefore, control plot basal area during year zero (2013) defined initial stand density prior to thinning.

At each location, three comparable 0.04 hectare (tenth acre) measurement plots were established. Each 0.04 hectare measurement plot was located within a 0.2 hectare (half acre) treatment plot which acted as a buffer. Treatments were randomly applied to each plot conducted during the summer of 2013, including a control (no thinning), 544 trees per hectare (4.3 m spacing), and 321 trees per hectare (5.5 m spacing). The 4.3 m spacing treatment was selected to represent "operational" spacing, and the 5.5 m spacing was selected to determine how the additional removal of competition impacted resource availability. Thinning favored dominant and healthy Douglas-fir trees at approximately equal interval spacing. Study locations were mixed species forests, of which Douglas-fir was dominant, representing from 48% to 98% of the total plot basal area (Table 1). Other common species present at study locations included grand fir, western red cedar, western larch (*Larix occidentalis* Nutt.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and lodgepole pine (*Pinus contorta* Dougl. ex. Loud.), none of which represented more than 36% of the total basal area.

2.2. Site characteristics

Site characteristics were determined using a combination of topographic, soil, and climate variables. We measured soil properties at three random locations in each plot using a bulk density sampler and soil auger. Measurements included bulk density, depth of Mount Mazama volcanic ash (McDaniel et al., 2005), duff layer depth, and soil classification. Parent materials and soil classification were determined through site observations and verified using United States Geological Survey (USGS) maps and Natural Resource Conservation Service (NRCS) soil surveys (USDA NRCS,

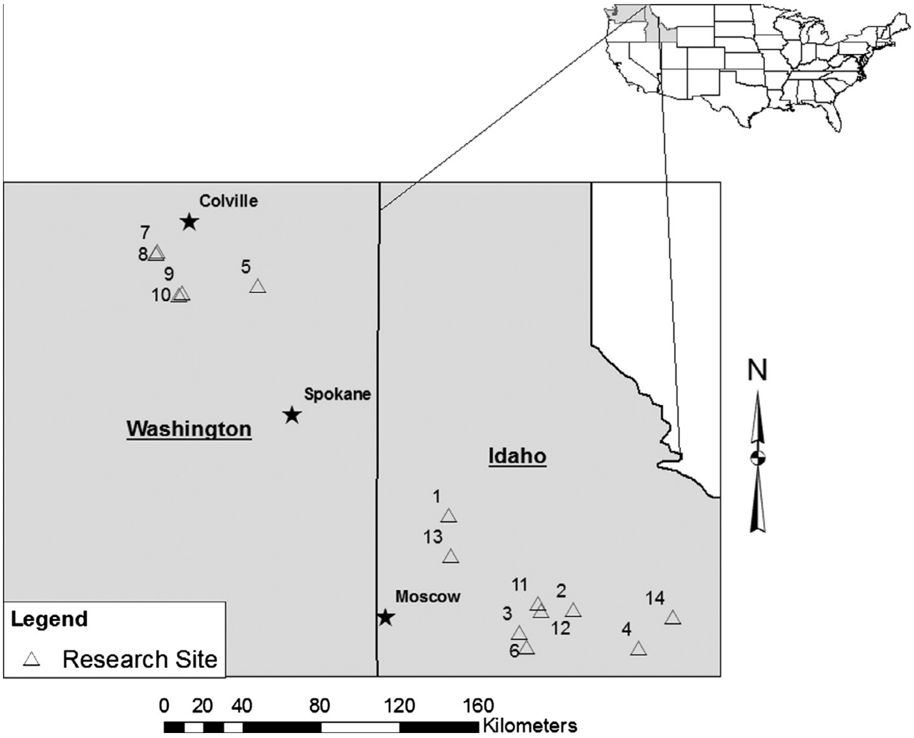

Fig. 1. Map of research locations.

Table 1
Initial stand characteristics for the fourteen research locations ordered from lowest to highest basal area. Bold and underlined stands had data loggers and ion exchange resins installed.

Stand	Basal area (m^2 ha^{-1})	Productivity (m $decade^{-1}$)	Stand age (years)	Trees (ha^{-1})	QMD[a] (cm)	SDI[b]	Volume (m^3 ha^{-1})	Proportion Douglas-fir (% of total basal area)
3	9.12	7.28	15	1730	8.19	290	17.97	67
12	9.62	6.46	14	3558	5.87	350	10.52	84
13	11.85	6.86	18	3682	6.40	416	27.78	85
4	13.61	7.41	16	2323	8.64	424	24.45	92
8	14.54	5.49	30	3385	7.39	482	21.16	69
2	18.49	7.74	19	2471	9.76	549	57.97	91
14	19.66	6.89	16	4547	7.42	651	31.11	74
7	20.50	5.24	30	7636	5.85	747	24.76	81
9	22.01	5.12	29	2076	11.62	609	35.87	98
11	23.50	7.28	20	8624	5.89	854	32.93	49
5	25.62	5.76	26	3064	10.32	744	55.93	66
10	25.95	5.24	29	6054	7.39	861	40.99	48
1	26.03	7.74	28	1112	17.26	615	57.37	93
6	28.37	6.83	20	8303	6.60	985	24.32	68

[a] QMD is the quadratic mean diameter of the measurement plot ((Basal area per hectare/trees per hectare)/0.00007854)^0.5.

[b] SDI is the stand density index, trees per hectare * (QMD/25)$^{1.6}$ (Reineke, 1933).

2014). We classified parent materials using standardized weathering potential (low, medium, high) for the region based on chemical and mineralogical analyses (Garrison-Johnston et al., 2003; Kimsey et al., 2008). We acquired climate data including mean annual precipitation (MAP) and mean annual temperature (MAT) from the ClimateWNA model using the latitude, longitude, and elevation of plot locations (Wang et al., 2012) (Table 2).

2.3. Tree growth

We recorded tree diameters and species on all trees above breast height (1.37 m) in every plot during dormancy for the fall of both 2013 and 2014. We selected a stratified random subsample of five trees per 1-in. diameter class to make more detailed tree measurements on control plots. All trees in thinned plots received detailed measurements. Detailed measurements included total height and the height to the base of the live crown taken one year after PCT (2014) using a TruPulse™ 200B hypsometer (Laser Technology Inc., Centennial CO). Crown classes were assigned based on the position and size of the tree crown within the overall canopy. We developed height to diameter regressions from subsampled trees for control plots, and used them to estimate height of unmeasured trees. The 10 largest trees in each plot (247 trees ha^{-1}) defined the "crop" trees at a location. We determined the crown ratio of crop trees by subtracting the height to base of live crown from the total height, then dividing by the total height. We calculated volume for each species using equations from Wykoff et al. (1982).

Table 2
Site characteristics for the fourteen research locations ordered from lowest to highest basal area. Bold and underlined sites had data loggers and ion exchange resins installed.

Stand	MAT[a] (°C)	MAP[b] (mm)	Elevation (m)	Habitat type[c]	Ash depth (cm)	Soil bulk density (g cm^{-3})	Parent material	Rock weathering
3	6.5	1043	1035	THPL/ASCA	51	0.73	Gneiss	Medium
12	6.9	1024	932	THPL/CLUN	52	0.65	Tertiary sediments	High
13	7.4	876	900	TSHE/ASCA	57	0.80	Quartzite	Low
4	6.3	1232	1169	THPL/ASCA	49	0.72	Mica schist	Medium
8	5.8	646	1185	THPL/CLUN	37	0.76	Glacial	Low
2	6.3	1115	1036	THPL/ASCA	56	0.84	Schist	Medium
14	6.6	1343	1075	THPL/ASCA	72	0.58	Granitic	Medium
7	5.7	641	1233	ABGR/LIBO	41	0.90	Glacial	Low
9	6.4	787	1097	THPL/CLUN	36	0.77	Glacial	Low
11	6.2	1098	1045	THPL/CLUN	58	0.78	Gneiss	Medium
5	6.3	733	983	TSHE/CLUN	40	0.90	Quartzite	Low
10	5.9	822	1162	ABGR/CLUN	42	0.73	Glacial	Low
1	7.3	793	1006	THPL/ASCA	41	0.92	Siltite-argillite	Medium
6	7.1	885	1027	THPL/CLUN	80	0.54	Schist	Medium

[a] MAT is mean annual temperature.

[b] MAP is mean annual precipitation.

[c] THPL: Western red cedar (*Thuja plicata* Donn ex D. Don), TSHE: Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), ABGR: grand fir, ASCA: wild ginger (*Asarum caudatum* Lindl.), CLUN: queencup beadlily (*Clintonia uniflora* (Menzies ex Schult. & Schult. f.) Kunth), LIBO: twinflower (*Linnaea borealis* (Forbes) Hultén ex R.T. Clausen).

2.4. Physical resources

Physical resource measurements included light, water, and temperature. We measured photosynthetically active radiation (PAR) on all plots during peak sunlight hours in mid-summer after PCT treatments. PAR readings were taken every meter on four random transects through each plot using a SunScan SS1 ceptometer (Delta-T Devices Ltd., Cambridge U.K.). A BF3 beam fraction sensor simultaneously measured total PAR at a nearby opening receiving full sunlight. Intercepted radiation was the difference between total and in-plot PAR measurements. Six locations had Em5b data loggers, with two EC5 soil volumetric water content (VWC) sensors and either two RT-1 temperature sensors wired to the logger (Decagon Devices Inc., Pullman WA), or two self-logging temperature sensors (DS1921G Thermocron iButton, Maxim Integrated Products Inc., San Jose CA). Moisture and temperature sensors were installed 15 cm below the soil surface, recording measurements every three hours in each plot. The VWC at permanent wilting point (PWP) was determined by using the 1500 kPa of the <2 mm fraction of soil from the NRCS soil survey (NRCS, 2014). The remaining eight sites only had two self-logging temperature sensors at 15 cm depth at each plot (DS1921G Thermocron iButton, Maxim Integrated Products Inc., San Jose CA). At the eight sites without moisture sensors, three to five randomly distributed spot soil VWC readings were taken 15 cm below the soil surface using a TRIME-FM3 (IMKO GMBH, Ettlingen Germany) or a Hydrosense™ (Campbell Scientific Inc., Logan UT) time domain reflectometer. We took spot soil moisture readings during the fall, spring, and summer after treatment. Winter spot soil moisture measurements were not taken because sites were inaccessible.

2.5. Nutrient availability

Soil nutrient availability included extractable soil nutrients and nutrients in the soil solution. At all locations, we collected soil samples during the summer of 2014 using a bulk density sampler, and allowed them to air dry for approximately 28 days. The University of Idaho Analytical Sciences Laboratory (Moscow ID) analyzed soil samples using the following methods. Soil pH was measured using an electrode in a 1:1 soil to water saturated paste. Nitrate (NO_3) and ammonium (NH_4) were extracted using potassium chloride (KCl) and measured colorimetrically with a spectrometer. Phosphorous (P) and potassium (K) were extracted using sodium acetate (CH_3COONa) and measured colorimetrically using a spectrometer and a flame photometer, respectively. Sulfur (S) was extracted with calcium phosphate and measured using ion chromatography. Boron (B) was prepared using a hot water extraction and measured colorometrically using a spectrometer. Organic matter was prepared with a solution of dichromate and sulfuric acid (H_2SO_4) and measured colorimetrically with a spectrometer. We converted soil nutrient concentrations ($\mu g\ g^{-1}$) to content ($\mu g\ cm^{-3}$) using average bulk density ($g\ cm^{-3}$) for each plot. The six sites with data loggers had five ion exchange resin capsules installed in each plot measuring available nutrients in solution (Unibest Inc., Walla Walla WA). We installed ion exchange resins at a depth of 15 cm during late summer 2013, and removed them during mid-summer 2014. Unibest extracted resin capsule nutrients with 50 mL hydrochloric acid (HCl) using the drip method. Nitrate and ammonium analyte concentration was measured using a flow injection analyzer. All other nutrients were measured using inductively coupled plasma optical emission spectroscopy. Ion exchange resin capsule values were converted to $\mu g\ cm^{-2}$ using the surface area of each capsule to represent the total amount of nutrients captured by each capsule. Resin capsule analytes included NO_3, NH_4, aluminum (Al), B, calcium (Ca), copper (Cu), iron (Fe), K, magnesium (Mg), manganese (Mn), sodium (Na), P, S, and zinc (Zn).

Foliar nutrient characteristics were determined from foliage collected in the field and processed in the laboratory. We sampled four sunlit branches from the top third of the crown of five randomly selected dominant Douglas-fir trees in each plot using a pruning poll. After collection, foliage was transported to the laboratory on ice then frozen to minimize water loss during processing. For leaf area, a digital image was taken of 100 current-year needles composited from each tree on a treatment plot (PowerShot SX40 HS, Canon U.S.A. Inc., Melville NY). The image was then analyzed with Image J software to measure the area of needles (Abràmoff et al., 2004). Needles were subsequently dried at a temperature of 65 °C for 48 h, then ground. Harris Laboratories (Lincoln NE) measured total Kjeldahl N using flow injection analysis. For all other macro (P, K, Mg, Ca, S) and micro (Zn, Mn, Cu, Fe, B, Al) nutrients, the foliage was digested in nitric acid, then analyzed using inductively coupled plasma spectrometry. Foliar nutrients were vector-analyzed to simultaneously compare concentration, content, and needle weights (Timmer and Stone, 1978).

2.6. Statistical analysis

Tree growth and physiochemical response variables were analyzed with Analysis of Covariance. We defined tree growth using both total 1-year plot basal area growth and mean basal area growth of the 10 largest trees per plot. We averaged soil moisture and temperature data from both spot measurements and data loggers by plot and season. Soil and resin capsule nutrients and foliar micronutrients were logarithmically transformed to normalize the data. For presentation purposes, the "lsmeans" package in R back-transformed means (Lenth and Hervã, 2015). We first included 10-year height growth (site quality) and initial stand basal area (density) as covariates to determine their impact on thinning response. We also added climate, site, and stand covariates to control for additional variation using correlation matrices and stepwise Bayesian Information Criterion (BIC) selection. We tested interactions using Type III sums of squares and main effects with Type II sums of squares using the "car" package in R (Fox and Weisberg, 2011). Tukey's multiple comparisons of means provided adjusted means and standard errors for models with no thinning treatment interactions ("multcomp" package, Hothorn et al., 2008). We tested interactions between covariates and treatments at the first and third quartile of the covariate using the "effects" package in R (Fox, 2003). Data were analyzed using R studio (version 0.98.942, R Core Team, 2013).

3. Results

3.1. Tree growth

Tree and plot growth responded to thinning and initial stand conditions. Total plot basal area growth decreased 27% in the 4.3 m spacing, and 43% in the 5.5 m spacing relative to the control (Table 3, Fig. 2a). Total plot basal area growth was also influenced by initial plot basal area (basal area 0) and the interaction between initial basal area and site productivity (Table 3). Plot growth increased from 71% to 119% with corresponding changes in both initial basal area (10–20 m^2 ha^{-1}) and site productivity (5.5–7.5 m $decade^{-1}$). Crop tree basal area growth increased by 23% in the 4.3 m spacing and 56% in the 5.5 m spacing compared to controls (Fig. 2b). Site productivity explained 56% of the variation in crop tree growth (Table 3). Crown ratio was 3% higher in the 4.3 m spacing and 6% higher in the 5.5 m spacing than the control. Crown ratio increased with site productivity, but decreased at higher initial stand basal areas (Table 3).

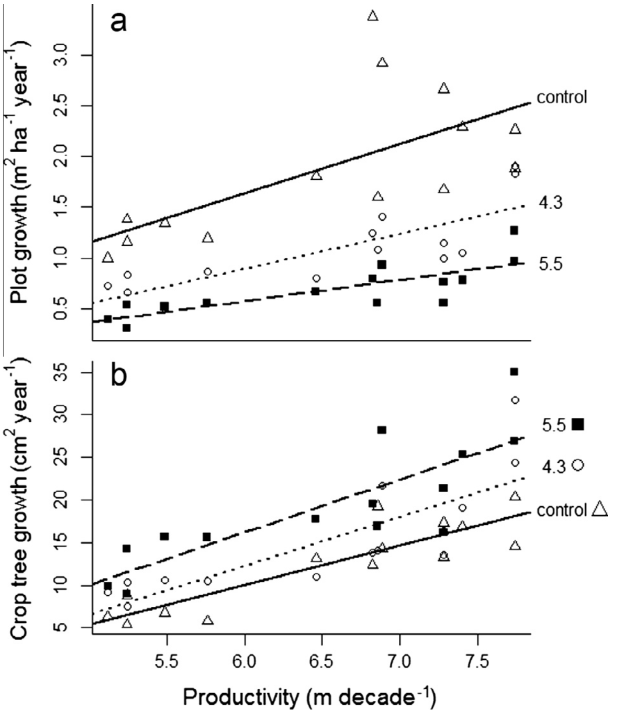

Fig. 2. Plot basal area growth (a), and crop tree growth (b) one year after thinning across a range in site productivity.

3.2. Physical resource response

Intercepted photosynthetically active radiation decreased after thinning and increased with initial stand basal area (Table 4). There was a 33% iPAR decrease in the 4.3 m spacing, and a 58% decrease in the 5.5 m spacing, compared to the control (Fig. 3). While it appeared that differences in iPAR due to thinning increased with initial basal area, the trend was not significant (D × T in Table 4). Soil VWC during the spring was 13% higher in the 4.3 m spacing and 18% higher in the 5.5 m spacing than the controls (Table 4), and increased by 18% as site productivity increased from 5.5 to 7.5 m $decade^{-1}$. Soil VWC in the summer was 51% higher in the

Table 3
Statistical analysis of the effects of site productivity (P), density (D), and thinning (T) and their interactions on plot and crop tree growth. Bold text indicates significance at $\alpha = 0.1$. Means and Tukey's multiple comparisons of means for each treatment appear below. Treatment means followed by the same letter are not significantly different at $\alpha = 0.1$.

Source	Plot growth (m^2 ha^{-1} $year^{-1}$)		Crop tree growth (cm^2 $year^{-1}$)		Crown ratio	
	r[A]	p[B]	r	p	r	p
P	0.463	0.380	0.747	**<0.001**	0.468	0.138
D	0.113	0.598	−0.071	0.417	−0.645	**0.005**
T		**0.006**		**<0.001**		**0.180**
P × D		0.686		0.812		**0.023**
P × T		0.698		0.668		0.949
D × T		0.397		0.696		0.701
P × D × T		0.452		0.723		0.739
Basal area 0	0.722	**0.018**				
P × basal area 0		**0.002**				
R^2[#]	0.8133		0.713		0.629	
Control	1.586 a		12.434 a		0.815 a	
4.3	1.159 b		15.253 a		0.839 a	
5.5	0.904 c		19.397 b		0.862 b	

[A] Pearson correlation coefficient (r).
[B] P value from the ANCOVA (p).
[#] R squared value of the linear model (R^2). R^2 values include only variables significant at $\alpha = 0.1$.

Table 4
Effects of site productivity (P), density (D), thinning (T), and their interactions on soil moisture and temperature. Bold text indicates significance at $\alpha = 0.1$. Means and Tukey's multiple comparisons of means for each treatment appear below. Treatment means followed by the same letter are not significantly different at $\alpha = 0.1$.

Source	iPAR (μmol m^{-2} s^{-1})		Spring VWC (cm^3 cm^{-3})		Summer VWC (cm^3 cm^{-3})		Spring temp (°C)		Summer temp (°C)	
	r[A]	p[B]	r	p	r	p	r	p	r	p
P	0.022	0.500	0.386	**0.009**	0.127	0.219	0.467	**0.016**	0.460	**0.001**
D	0.152	**0.048**	0.052	0.379	0.202	0.142	−0.088	0.164	0.029	0.370
T		**<0.001**		**0.092**		**0.002**		**0.055**		**0.011**
P × D		0.293		0.986		0.445		0.154		0.646
P × T		0.386		0.982		0.853		0.360		0.708
D × T		0.128		0.509		0.869		0.263		0.604
P × D × T		0.558		0.972		0.899		0.258		0.574
Elevation							−0.516	**0.009**		
Sine (aspect)							0.348	**0.009**		
R^2[#]	0.765		0.190		0.233		0.450		0.330	
Control	1389.684 a		0.379 a		0.157 a		5.224 a		12.869 a	
4.3	929.341 b		0.428 ab		0.237 b		5.716 ab		13.613 b	
5.5	585.134 c		0.447 b		0.273 b		5.883 b		13.775 b	

[A] Pearson correlation coefficient (r).
[B] P value from the ANCOVA (p).
[#] R squared value of the linear model (R^2). R^2 values include only variables significant at $\alpha = 0.1$.

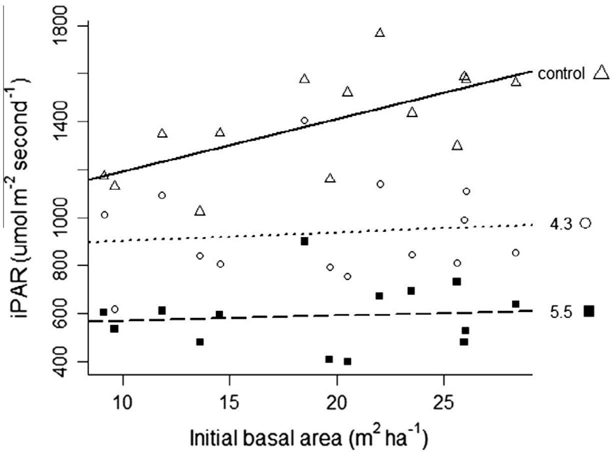

Fig. 3. Intercepted photosynthetically active radiation (iPAR) by treatment and initial stand basal area.

4.3 m spacing and 74% higher in the 5.5 m spacing relative to the control without any covariate correction. Soil temperature in the spring increased by 9% in the 4.3 m spacing and 13% in the 5.5 m spacing compared to controls. In the summer, soil temperature was 6% warmer in the 4.3 m spacing, and 7% warmer in the 5.5 m spacing than controls. Soil temperatures increased with productivity in both the spring and summer, but elevation and aspect also influenced spring temperature. Spring soil temperatures were warmer on more easterly aspects (sine of aspect, Table 4), with little difference in north–south aspects (cosine of aspect $p = 0.670$).

3.3. Nutrient availability response

Both soil and foliar nutrients responded to initial stand conditions and PCT. Total extractable inorganic soil N ($NO_3 + NH_4$) was 62% higher in the 4.3 m spacing and 36% higher in the 5.5 m spacing than the control, and increased with both initial basal area and site productivity (Table 5). A majority of total N was in the form of NH_4, which increased with both initial basal area and site productivity, but not with thinning treatment (Table 5). Soil NO_3 however, was 157% higher in the 4.3 m spacing and 171% higher in the 5.5 m spacing compared to the control, and increased with both precipitation and soil bulk density (Table 5). Soil S was 20% higher in the 4.3 m spacing treatment than either the 5.5 or control and increased by 23% as site productivity went from 5.5 to 7.5 m decade^{-1} (Table 5). Resin capsule S and B were highest in the control plots, then declined with increasing tree spacing (Table 5). Resin S was 3.2 μg cm^{-2} lower than the control in the 4.3 m spacing, and 4.4 μg cm^{-2} lower in the 5.5 m spacing (Table 5). Resin capsule B was 8% lower in the 4.3 m spacing and 20% lower in the 5.5 m spacing than the control. Resin capsule B correlated positively with ash depth and initial basal area (Table 5).

Pre-commercial thinning influenced Douglas-fir needle weights and foliar nutrients in a variety of ways. Douglas-fir foliar nutrients were not deficient for K, Ca, B, or Cu but were deficient in N, P, and S when compared with critical nutrient concentrations (Webster and Dobkowski, 1983). Based on foliar analysis, thinned stands were more N deficient, no longer P deficient, and more deficient in S for the 5.5 m spacing but less S deficient in the 4.3 m spacing than controls. Dominant Douglas-fir needle weight increased by 15% in the 4.3 m spacing and 12% in the 5.5 m spacing treatments when compared to the control, and increased with site productivity ($r = 0.337$, $p = 0.016$). Foliar N decreased by 5% in concentration, but increased by 5% in content on thinned plots (Fig. 4). Foliar N concentration increased at higher site productivities (Table 6). Other nutrients had little or no change in concentration (K, S, Cu; $p \geqslant 0.446$) but increased in content after thinning treatment (Fig. 4; $p < 0.1$). Foliar Cu content was higher in denser stands (Table 6), but foliar S content had no relationship with productivity or density ($p \geqslant 0.642$). The foliar K content in the 4.3 m spacing was 13% higher than the 5.5 m spacing, and 22% higher than the control at low productivity locations (5.5 m decade^{-1}). However, there was only a 4% difference in foliar K between treatments at high productivity locations (7.5 m decade^{-1}, P × T $p = 0.095$).

Other foliar nutrients either increased or decreased in both nutrient concentration and content in response to PCT. Foliar Ca, and Zn contents and concentrations declined in thinned plots compared to controls (Fig. 4), which indicates excess based on vector analysis (Haase and Rose, 1995). While both foliar Ca and Zn concentrations were negatively influenced by site productivity, foliar Zn was also influenced by elevation (Table 6). In contrast, thinning positively influenced foliar concentrations and contents of both P and B; suggesting deficiencies according to vector analysis. At lower productivity sites (5.5 m decade^{-1}), foliar P content declined 27% with increasing density (10–25 m^2 ha^{-1}) but at higher productivity sites (7.5 m decade^{-1}), foliar P content increased by 13% from low to high density (P × D $p = 0.029$). Foliar B content increased at higher elevations, but decreased as precipitation increased (Table 6).

Table 5

Effects of site productivity (P), density (D), thinning (T), and their interactions on soil nutrient availability. Bold text indicates significance at $\alpha = 0.1$. Means and Tukey's multiple comparisons of means for each treatment appear below. Treatment means followed by the same letter are not significantly different at $\alpha = 0.1$.

Source	Total N (μg cm^{-3})		NH$_4$ (μg cm^{-3})		NO$_3$ (μg cm^{-3})		Soil S (μg cm^{-3})		Resin S (μg cm^{-2})		Resin B (μg cm^{-2})	
	r[A]	*p*[B]	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
P	0.312	**0.003**	0.229	**0.020**	0.224	0.104	0.268	**0.070**	0.315	0.135	−0.268	0.383
D	0.389	**0.001**	0.249	**0.040**	0.314	0.294	0.057	0.553	0.060	0.600	0.607	**0.030**
T		**0.015**		0.172		**0.044**		**0.076**		**0.054**		**0.046**
P × D		0.610		0.403		0.508		0.367		0.189		0.404
P × T		0.865		0.745		0.519		0.781		0.674		0.881
D × T		0.828		0.733		0.142		0.673		0.653		0.893
P × D × T		0.915		0.705		0.971		0.653		0.660		0.934
MAP					0.089	**0.008**						
Bulk density					0.134	**0.010**						
Duff depth									0.152	**0.061**		
Ash depth									0.716	**<0.001**	0.319	**0.001**
Rock weathering											−0.138	**0.007**
R^2[#]	0.347		0.173		0.240		0.128		0.661		0.624	
Control	10.357 a		8.366 a		1.003 a		1.999 ab		14.636 a		0.143 a	
4.3	16.807 b		11.049 a		2.578 b		2.388 b		11.482 ab		0.130 ab	
5.5	14.035 a		8.897 a		2.716 b		1.961 a		10.199 b		0.113 b	

[A] Pearson correlation coefficient (*r*).

[B] *P* value from the ANCOVA (*p*).

[#] *R* squared value of the linear model (R^2). R^2 values include only variables significant at $\alpha = 0.1$.

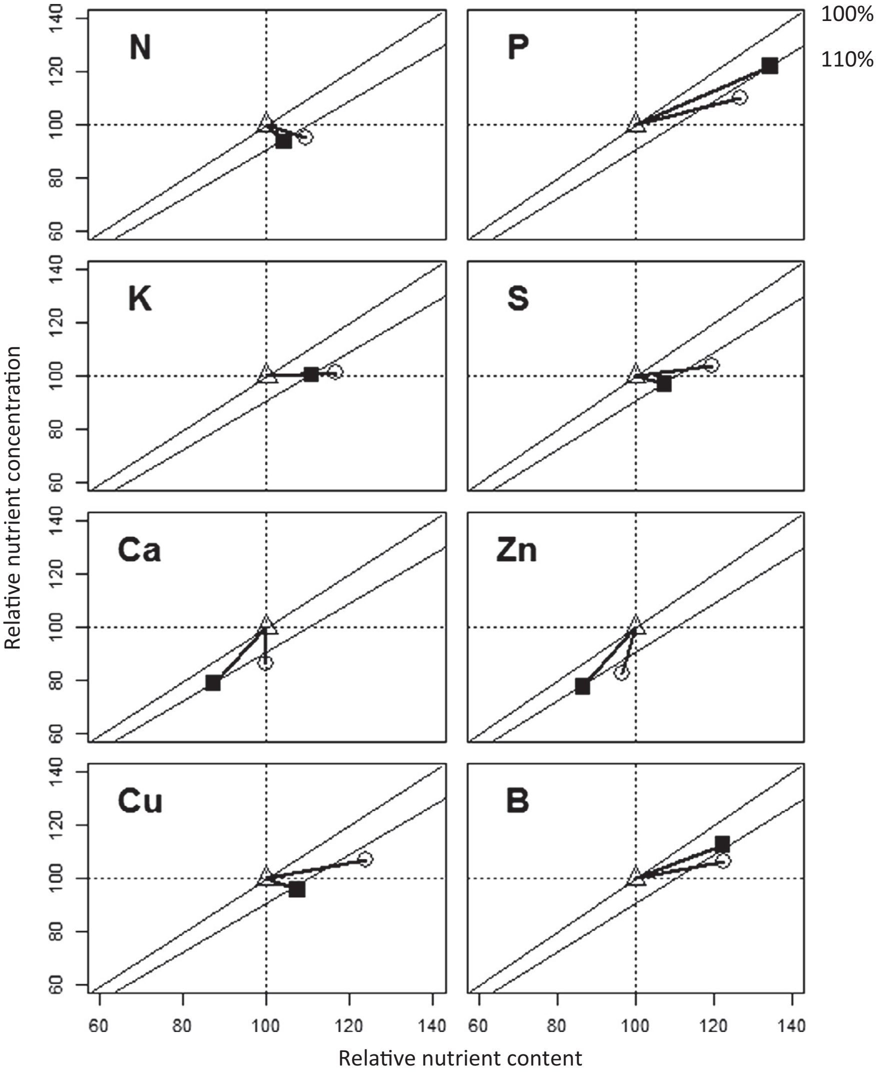

Fig. 4. Vector analysis for foliar nutrients by treatment, all units are relative to control (100). Treatments include a control (△), 4.3 m spacing (○) and 5.5 m spacing (■). Diagonal lines represent no change (100%) or a 10% increase (110%) in needle weights relative to controls.

Table 6
Statistical analysis of site productivity (P), density (D), and thinning (T) on foliar nutrient concentrations and content. Nutrients presented had significant main effects of thinning treatment. Means and Tukey's multiple comparisons of means for each treatment are presented below. Bold text indicates significant differences at $\alpha = 0.1$. Treatment means followed by the same letter are not significantly different at $\alpha = 0.1$.

Source	[N] (g kg^{-1})		[P] (g kg^{-1})		[Ca] (g kg^{-1})		[Zn] (mg kg^{-1})		Cu content (μg 100 needles^{-1})		B content (μg 100 needles^{-1})	
	r[A]	p[B]	r	p	r	p	r	p	r	p	r	p
P	0.233	**<0.001**	−0.574	**<0.001**	−0.432	**0.002**	−0.432	**0.076**	0.108	0.209	−0.233	0.179
D	−0.174	0.377	−0.083	**0.095**	0.206	0.324	0.097	0.900	0.367	**0.014**	0.198	0.287
T		**0.020**		**0.003**		**0.006**		**0.053**		**0.085**		**0.029**
P × D		0.948		0.135		0.260		0.117		0.141		0.391
P × T		0.343		0.193		0.678		0.244		0.552		0.119
D × T		0.340		0.303		0.777		0.254		0.692		0.313
P × D × T		0.290		0.264		0.810		0.231		0.566		0.202
Elevation	0.459	**<0.001**					0.590	**<0.001**			0.341	**0.030**
MAP											−0.384	**0.013**
R^2[#]	0.475		0.484		0.329		0.426		0.180		0.298	
Control	10.03 a		1.50 a		4.82 a		2.914 a		2.281 a		16.904 a	
4.3	9.60 ab		1.65 ab		4.17 b		2.773 ab		2.730 b		20.595 b	
5.5	9.40 b		1.84 b		3.80 b		2.696 b		2.426 ab		20.570 b	

[A] Pearson correlation coefficient (r).
[B] P value from the ANCOVA (p).
[#] R squared value of the linear model (R^2). R^2 values include only variables significant at $\alpha = 0.1$.

4. Discussion

4.1. Tree growth

The difference between plot basal area growth on control plots and thinned plots was greatest at higher site productivity (Fig. 2a). This relationship is not surprising because we defined site quality by tree growth. However, the knowledge that thinned stands at higher productivities responded better to thinning than stands at lower productivities suggests that forest managers wanting to maximize stand basal area growth should prioritize high productivity locations for thinning. Other research shows similar basal area growth responses to both fertilization and thinning in the region (Brockley, 2005), but our experiment is unique in looking at inherent site quality or productivity. Similarly, dominant tree growth increased slightly more on thinned plots at high productivities than thinned plots at low productivities compared to controls (Fig. 2b). Faster growth rates for the largest trees in a stand are common after pre-commercial thinning (Brissette et al., 1999; Pothier, 2002). Our results suggest that thinning high productivity stands may further improve the growth of the larger crop trees than thinning low productivity stands (Fig. 2b). Changes in crop-tree crown ratios were observed just one year after thinning, even though they were relatively small. Previous research has demonstrated that higher crown ratios in response to thinning are common; although generally over longer time scales (Brix, 1981; Brockley, 2005). It is possible that measurement error influenced changes in the crown ratio due to difficulty seeing branches in denser control plots.

4.2. Physical resources

Intercepted photosynthetically active radiation (iPAR) expressed an interesting pattern. Thinned plots averaged 65% higher iPAR per m^2 of basal area than controls, indicating higher light interception efficiency. Higher competition should have resulted in smaller crowns compared with those grown under low density. However, on thinned plots, iPAR did not decline with increasing initial stand density (Fig. 3). This result also suggests there would be no loss of growth potential for residual trees in high density stands following thinning due to the strong relationship between productivity and intercepted radiation (Landsberg et al., 1997). Supporting this finding, Will et al. (2001) found strong correlations between intercepted radiation and stand volume growth in stands of various densities. As the forest canopy develops over time, stand leaf area and light interception in thinned plots will increase and become similar to controls (Drew and Flewelling, 1979; Medhurst and Beadle, 2001). Despite the focus of many studies on increased availability of light after thinning (Tang et al., 1999; Will et al., 2001), the iPAR response to thinning in our study was lower than that of other resources.

Pre-commercial thinning significantly increased summer soil water conditions (Table 4). However, it is difficult to distinguish if the increased soil moisture was caused by less evapotranspiration from the removed trees (Stogsdill et al., 1992) or increased slash loading (Smethurst and Nambiar, 1990) as slash was retained on all plots and water use was not measured. To separate the effects of slash and vegetative competition on soil moisture, it would be necessary to measure transpiration, and precipitation throughout the season. Regardless, residual trees on thinned plots are likely less water-stressed than those in control plots (Aussenac and Granier, 1988). However, these advantages dissipate as the residual trees increase leaf area and demand for water resources (Moreno and Cubera, 2008; Sohn et al., 2013), particularly during drought conditions (Bréda et al., 1995; D'Amato et al., 2013). Soil VWC in the spring increased with both productivity and thinning treatment signifying higher productivity stands received a greater spring soil moisture benefit from PCT than lower productivity stands (Table 4). Higher soil moisture in the spring is an important predictor of Douglas-fir growth (Littell et al., 2008). In contrast, soil VWC in the summer was independent of both initial density and productivity. Annual drought occurs throughout the region, and by mid-summer available soil moisture was low in both moist and dry sites. Based on summer soil moisture, one cannot predict the length of time before depletion, or the length of favorable growing conditions. When soil moisture data from data loggers were examined, we observed that the mean VWC of the control plots reached the permanent wilting point (PWP) on July 28th of 2014, at which point the 4.3 m spacing had 41% higher VWC and the 5.5 m spacing had 105% higher VWC. The mean VWC of the 4.3 m spacing plots did not reach the PWP until September 9th of 2014, 43 days after the control, and the 5.5 m spacing plots

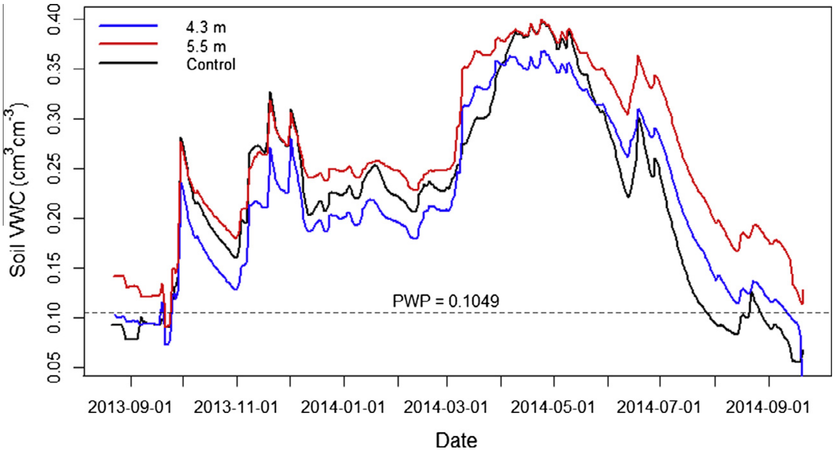

Fig. 5. Mean daily soil moisture by spacing treatment for six locations with data loggers in the Inland Pacific Northwest. PWP is the mean permanent wilting point for the <2 mm fraction of soil across all six locations (NRCS, 2014).

did not reach the PWP during the 2014 measurement period (Fig. 5). After thinning, higher summer soil VWC improved drought conditions and potentially lowered tree water stress, as similarly found by Bréda et al. (1995).

Higher soil temperatures in thinned plots during the spring could initiate an earlier start to the growing season. Spring soil temperatures were warmer on more easterly aspects, with little difference in north–south aspects. Soils on easterly aspects could be warmer due to greater direct sunlight in the morning when the sun is in the east. Soil temperatures were positively correlated with productivity, suggesting that more productive sites have warmer soil temperatures throughout the spring and summer (Table 4). Stage (1976) demonstrated higher western white pine site index or productivity on warmer easterly slopes than on other aspects, particularly at slopes above 30%. Furthermore, at higher soil temperatures, N mineralization likely increases unless limited by other factors such as moisture (Powers, 1990; Chmura et al., 2011).

4.3. Nutrient availability

Extractable N in the soil increased after thinning, but declined in foliar concentration. Most N mineralization and ion mobility in the soil occurs when the soil is moist and warm, such as after thinning (Powers, 1990). Other research observes an increase in inorganic soil N (NO_3 and NH_4) after PCT, which improves forest growth (Brix, 1981; Forrester et al., 2012) and pest resistance (Stoszek et al., 1981). Our results also showed increased levels of extractable inorganic N, particularly for the 4.3 m spacing (Table 5). However, soil N measured at one point in time may differ from what is actually available to trees because N pools are in constant flux (Davidson et al., 2000; Smethurst and Nambiar, 1990). Resin capsules in the 4.3 m ($3.09\ \mathrm{g\ N\ cm^{-2}}$) and 5.5 m ($3.13\ \mathrm{g\ N\ cm^{-2}}$) spacing did acquire slightly more N than the control ($3.08\ \mathrm{g\ N\ cm^{-2}}$), however these differences were not significant. More resin capsules in each plot and across all locations may provide more clarity to N differences between thinning treatments. Contrary to the 16% increase in foliar N content found by Hokka et al. (1996), we did not detect significant changes in foliar N content; rather foliar N concentration decreased after thinning (Fig. 4). Higher foliar N concentration after thinning was found in Douglas-fir (Velazquez-Martinez et al., 1992), radiata pine (Carlyle, 1998), and balsam fir (Thibodeau et al., 2000), which disagree with our results and other research on loblolly pine (Ginn et al., 1991). Networks of mycorrhizal fungi could influence the short-term availability of nutrients to residual trees after thinning and may have played a role in nutrient redistribution (Simard et al., 1997). However, ectomycorrhizal fungi were not measured in this experiment and therefore their degree of influence on foliar nutrients is uncertain.

Phosphorous had the strongest response in the foliage compared to all other nutrients analyzed, but differences in the soil were not significant ($p \geqslant 0.132$). Other research demonstrates an increase in foliar P after pre-commercial thinning (Carlyle, 1995; Hokka et al., 1996; Thibodeau et al., 2000). One suggestion for this relationship is that leaching of P from slash left after PCT replaced the P immobilized by the trees (Sterba, 1988). The majority of the P acquired by trees is from organic soil horizons (Johnson et al., 2003; Yanai, 1992), which we did not sample. Although others have reported that P is not regionally deficient (Coleman et al., 2014), foliar P concentration was below critical levels at 10 out of the 14 locations in this study (Webster and Dobkowski, 1983). On average, thinning alleviated the P deficiency across all research locations. Alleviating P deficiency in Douglas-fir can improve growth rates, photosynthetic efficiency, and root hydraulic conductance (Coleman et al., 1990; Marschner, 1996).

Sulfur in the soil and foliage had an interesting response to thinning. Both the control and the 5.5 m spacing had lower sulfur values than the 4.3 m spacing (Table 5). This same pattern occurred for soil S and for foliage S concentration. In contrast, resin S was higher in the control than either the 4.3 or 5.5 m spacing. However, we do not consider our resin capsule data to be as reliable as soil or foliage data because of lower sample size and disagreement with other results (N and B). Based on foliage analysis, Douglas-fir was S deficient across all of the study sites, and increasing the S deficiency from thinning to 5.5 m spacing could have consequences for nutrient cycling processes and tree growth (Coleman et al., 2014). The mechanisms behind why the 4.3 m spacing had more soil S are unclear. The relationship between S and thinning intensity needs further research to test our results and improve mechanistic understanding.

Boron declined in the soil solution, but increased in the foliage. The amount of available B, determined through resin capsule analysis, decreased with thinning. However, foliar B was elevated in thinned plots, suggesting that residual trees are better able to acquire B after PCT operations. Potential explanations for the B decrease in solution but increase in foliage could be that plant roots acquired B before it reached the resin capsule at 15 cm depth, or that trees are better able to acquire B than the resin capsules. Although the stands studied in this experiment were not B deficient, B uptake still increased after thinning (Fig. 4). If this pattern holds, thinning could help alleviate B deficiencies that occur in

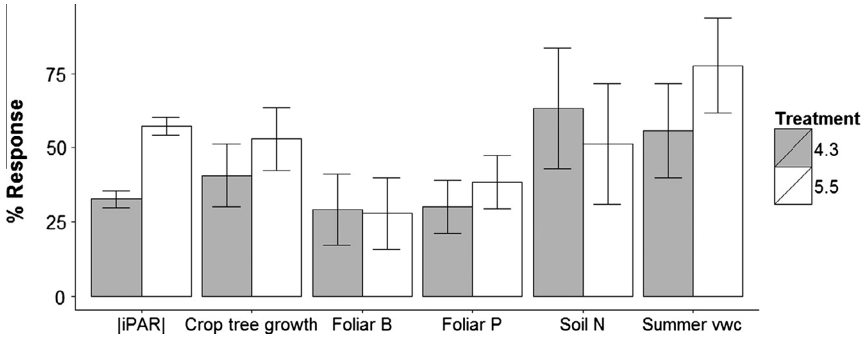

Fig. 6. Resource response to pre-commercial thinning relative to unthinned controls. The absolute value of iPAR is presented for meaningful comparison between resources.

roughly 20% of Douglas-fir stands throughout the Inland Northwest (Moore et al., 2004). Relieving the B deficiency in trees could provide better drought and cold tolerance and avoid stem form and wood quality problems (Lehto et al., 2010).

4.4. Research implications

Many studies focus on the availability of light throughout the canopy after thinning as the primary resource controlling photosynthetic or growth response of trees (Tang et al., 1999; Will et al., 2001). While iPAR had a strong relative response to thinning, relative soil moisture in the summer had the strongest response (Fig. 6). Others have found a positive response between available soil water after thinning, ponderosa pine growth, and stomatal conductance (McDowell et al., 2003; Sohn et al., 2014). The relative response of extractable soil N (NO_3 and NH_4) was comparable to that of light and moisture. Several studies corroborate that nutrient availability has a strong control on tree growth (Carlyle, 1998; Drever and Lertzman, 2001; Jokela et al., 2004). Future research should investigate the interactions between limiting resources and the individual amount of influence light, water, and nutrients have on tree growth.

Some resources showed strong trends with initial stand and site conditions (light and soil N), while others did not (summer soil moisture). Intercepted photosynthetically active radiation (iPAR) was greatest at stands with higher initial densities for control plots, but not for thinned plots (Fig. 3). Higher relative soil moisture in the summer happened regardless of the initial stand conditions (productivity or density). The relative response in extractable N was greatest in both denser and more productive stands (Table 5). The influence of initial site and stand conditions on resource response to pre-commercial thinning, and the magnitude of relative soil moisture and soil N, emphasize the need for considering multiple resources and locations when studying the forest response to density manipulations.

5. Conclusions

The results outlined in this paper suggest intricate relationships between resource availability, PCT, site, and stand characteristics. Improved light, moisture, and nutrients after thinning will decrease a suite of resource limitations, relieve multiple sources of stress for trees, and improve growth. Thinning high-density stands on low productivity sites will provide the greatest stress relief and benefit to forest health because resources are more limiting and competition is high. Alternatively, thinning high productivity, high density stands will maximize the growth response of residual trees. If resources for thinning operations are limited and the objective is to maximize growth, managers should prioritize higher rather than lower productivity stands to achieve the greatest thinning response. Our results suggest that for the studied forest types, soil moisture and nutrients had the strongest response to pre-commercial thinning, followed by light availability.

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