

Five-year growth, biomass, and nitrogen pools of Douglas-fir following intensive forest management treatments

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ABSTRACT

In young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) stands, intensive forest management has resulted in variable responses in survival and growth and therefore stand biomass due to effects on microclimate and competition for limited resources. As seedling genetics and management practices develop over time, there is a need to re-evaluate how Douglas-fir survival and growth varies with intensive practices. Five-year Douglas-fir diameter at 15 cm (D15) and height growth, biomass, and nitrogen (N) pools after organic matter removals and soil compaction at a recently established site in central Oregon (NARA) were compared to five-year results from three Douglas-fir sites with organic matter removal and vegetation control treatments that were established 10–14 years earlier in central Washington (Fall River and Matlock) and northern Oregon (Molalla). The NARA site contained up to two times greater individual-tree foliar and branch biomass for the same stem D15 than the previously established sites, possibly due to a lower planting density, a warmer climate, and/or improved genetics/different seed sources. Prediction of stem biomass was similar at all sites using $D15^{2.4} \times \text{height}$. Periodic D15 and height growth from 1 to 3 years and five-year Douglas-fir biomass was lower in the bole-only (BO) without compaction treatment at NARA compared to other treatment combinations. Greater periodic D15 and height growth after five years of annual vegetation control (Fall River, Matlock, and Molalla) resulted in larger Douglas-fir biomass compared to the initial vegetation control treatments. These results indicate the beneficial effects of vegetation control on early growth across a wide range of conditions. With one exception, whole-tree removal treatments did not affect five-year-old Douglas-fir biomass or N pools, indicating site resilience to increased OM removal across the region. A principal component analysis (PCA) clearly separated all four sites according to climate, soil temperature and moisture, N availability, D15 and height growth, and Douglas-fir and competing vegetation biomass. Within each site, the PCA showed that vegetation control was associated with the greatest differences in Douglas-fir and competing vegetation biomass. This supports the notion that site factors and vegetation control treatments are critically important in mitigating response to intensive management practices.

1. Introduction

Intensive forest management, including practices at stand establishment such as increased organic matter (OM) removal, competing vegetation control, and soil compaction, have the potential to increase Douglas-fir productivity but may also detrimentally affect soil properties and functions. In young forest stands (<5 years), effects of OM removal treatments have been attributed to temporary changes in microclimate, while stands at canopy closure appear to be more susceptible to nutrient losses associated with increased OM removal (Thiffault et al. 2011). In Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) stands in

the Pacific Northwest (PNW), removal of OM increased growing-season soil temperatures in the first five years after harvesting, which resulted in changes in nitrogen (N) mineralization and leaching rates (Licata, 2004; Strahm et al. 2005; Devine and Harrington, 2007). Across the Long-Term Soil Productivity (LTSP) network, seedling survival tended to increase after whole-tree and whole-tree plus forest floor removals due to improved microclimate and planting efficiency, but effects on seedling growth were not consistent (Fleming et al. 2006; Harrington and Schoenholtz, 2010; Thiffault et al. 2011; Ponder et al. 2012). Long-term effects of whole-tree removals on soil and site productivity appear to be related to the pre-treatment soil nutrient availability at individual

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sites (Thiffault et al. 2011; Littke et al. 2020a).

The effect of soil compaction on planted tree growth depends on soil texture such that increases in seedling growth were seen on sites with sandy soils and growth losses were found on sites with clayey soils (Gomez et al. 2002; Fleming et al. 2006; Ponder et al. 2012). Growth improvements on compacted coarse-textured soils were due to increased water holding capacity over uncompacted soils, while fine-textured soils reached permanent wilting point faster due to decreased soil porosity (Gomez et al. 2002). Shallow coarse-textured soil bulk densities also recovered faster than fine-textured soils five years after compaction (Page-Dumroese et al., 2006).

In the western PNW, coastal Douglas-fir is the main plantation tree species under intensive forest management. Douglas-fir productivity in the region is variable due to elevation, climate, soil development, and nitrogen availability (Steinbrenner 1979; Littke et al., 2016). Three Douglas-fir LTSP sites with varying soil nutrition (3,300–10,188 kg N ha⁻¹) and site productivity (36–42 m at 50 years) were established in 1999 and 2003 to understand the effects of OM removals and vegetation control on soil and site productivity under distinct climate and soil types (Ares et al., 2007; Harrington and Schoenholtz, 2010). Douglas-fir biomass components were positively related to diameter at 15 cm (D15) (foliar, branch, and total biomass) and D15*height (stem biomass) at five years after planting (Devine et al., 2011). All three sites fit the same allocation equations for each biomass component, but Douglas-fir biomass pools were unique between sites (Devine et al., 2011). Above-ground N pools and foliar N concentration were positively correlated with total soil N across all sites, but the amount of competing vegetation biomass differed by site and treatment. Even though biomass allocation was similar among the three sites, short-term (5–11 year) and long-term (15–20 year) results from these studies suggest that treatment effects on tree growth, soil and foliar nutrient concentrations, and biomass are variable among sites in the same region (Devine et al. 2011; Slesak et al., 2016; Littke et al., 2020a; Littke et al., 2020b). Given this, additional comparisons across a wider range of soil nutrition and climates are needed to fully understand the influence of intensive forest management on Douglas-fir growth in the PNW region.

In 2013, the Northwest Advanced Renewables Alliance (NARA) supported the establishment of an additional Douglas-fir LTSP site to understand the effects of OM removals and soil compaction on soil productivity (soil nutrients, water availability, and bulk density) and methods for removing OM for aviation biofuel and co-products. The NARA site was established 10 and 14 years later than the first three sites and received adjusted treatments based on knowledge gained from the original Douglas-fir LTSP sites and best tailored to the questions posed by the NARA program. The NARA site was established in central western Oregon which is generally warmer and drier with finer textured soils than northern latitudes of the PNW. In previous Douglas-fir research, southern latitudes in the PNW have been found to have greater soil water holding capacity, total soil N content, needle area, and fertilizer response and lower summer precipitation and surface soil carbon (C) to nitrogen (N) ratios (Littke et al., 2014a; Littke et al., 2014b; Littke et al., 2017). In addition, the NARA site was planted with improved second-generation genetic gain seedlings compared to the first-generation improved seedlings from the previous three sites, which could affect uptake of nutrients and biomass allocation to foliage, branches, and stem (Dwivedi et al., 2019; du Toit et al., 2020).

Given these improvements in genetic selection and differences in climate, soils, and treatments between NARA and the three previously established sites, periodic Douglas-fir diameter at 15-cm and height growth, aboveground biomass, and N pools were compared with the original 5-year results to evaluate variation in response across a wider range of conditions. We tested the following hypotheses: 1) NARA Douglas-fir biomass will fit previous allocation equations of five-year Douglas-fir (Devine et al., 2011), 2) whole-tree removal and vegetation control or soil compaction treatment combinations will significantly improve Douglas fir growth, biomass, and N pools similarly at all

sites, and 3) site variability due to climate, soil nutrition, and competing vegetation severity will affect positive responses to treatments in Douglas-fir growth and biomass.

2. Methods

2.1. Site description

The four sites used in this study are all installations in the LTSP network located in Washington and Oregon and are referred to as NARA, Fall River, Matlock, and Molalla (Fig. 1, Table 1). The NARA site is located near Springfield, OR (Fig. 1). The northern edge of NARA is mapped as a Kinney cobbly medial loam (Andic Humudept), the central portion of the site is mapped as Peavine silty clay loam (Typic Haplohumult), and the southeast edge is mapped as a Cumley silty clay loam (Oxyaquic Palehumult) (Soil Survey Staff, 2019). The geology is composed of tuffaceous sedimentary rocks with basaltic andesite and flow breccias from the Oligocene and Miocene Ages (Walter and Duncan, 1989). Prior to harvest at NARA the previous Douglas-fir stand had a site index of 37 m at 50 years (King 1966) (Table 1). Fall River (near Brooklyn, WA) is situated on the Pomona basalt flow with a component of volcanic ash and the soil series is classified as a Boistfort silt loam (Typic Fulvudand) (Ares et al., 2007; Soil Survey Staff, 2019) (Table 1). Fall River is the highest productivity site with a site index of 42 m on the previous stand. The lowest soil nutrition and available water storage was found at the Matlock site (near Matlock, WA) where glacial outwash was deposited during the Pleistocene period (Kruckeberg, 1991) and the soil series is classified as a Grove very gravelly loamy sand (Dystric Xerorthent) (Harrington and Schoenholtz, 2010; Soil Survey Staff, 2019) (Table 1). At Molalla (near Dodge, OR), the parent material is basic igneous agglomerate and the soil series is classified as a Kinney cobbly medial loam (Andic Humudept) (Harrington and Schoenholtz, 2010; Soil Survey Staff, 2019). Matlock and Molalla were measured to have the same site index on the previous stands (37 m), but current site index measured at age 15 was 26 m and 34 m, respectively (Littke et al. 2020a).

The OM removal treatments applied to all sites at the final felling of the previous stand in this study were bole-only harvest (BO: merchantable bole removed) and whole-tree harvest (WT: boles and crowns removed from previous stand) (Table 2). Fall River, Matlock, and Molalla received vegetation control treatments, which included initial vegetation control (IVC) applied post-harvest or five years of annual vegetation control (AVC) that differed by site (Ares et al., 2007; Harrington and Schoenholtz 2010). NARA received post-harvest and two years of herbaceous and hardwood vegetation control on all treatments (Gallo, 2016). At NARA, the BO and WT removal treatments were treated with soil compaction (labeled 'C') and without compaction (without a 'C'), and the whole-tree harvest with forest floor removed treatment (WTFF-AVC-C: all aboveground biomass removed) only received the compaction treatment. In the compaction treatments, any remaining harvest residue/branches were windrowed while the soil surface was compacted, and then harvest residue was redistributed. Compaction raised 0–15 cm bulk density from 0.63 to 0.65 g cm⁻³ to 0.71–0.78 g cm⁻³ one month after treatment (S. Holub, personal communication). At Fall River, soil compaction was applied only in the BO-AVC-C treatment with an increase of 0–10 cm bulk density from 0.56 g cm⁻³ in non-compacted plots to 0.69–0.82 g cm⁻³ in compacted plots (Ares et al., 2005). An additional OM removal treatment was applied at Fall River where coarse woody debris was removed along with the WT treatment (WT+-AVC: WT plus existing dead wood such as large legacy wood, surface red rot, and live and dead coarse woody debris >0.6 cm). Four treatment blocks were installed at Fall River, Matlock, and Molalla based on plot proximity. At NARA, blocks were defined by pre-planting total soil nitrogen content (Gallo, 2016). Each treatment combination contained a total of four replicates at each site (one per block). Background information and site-specific treatments for

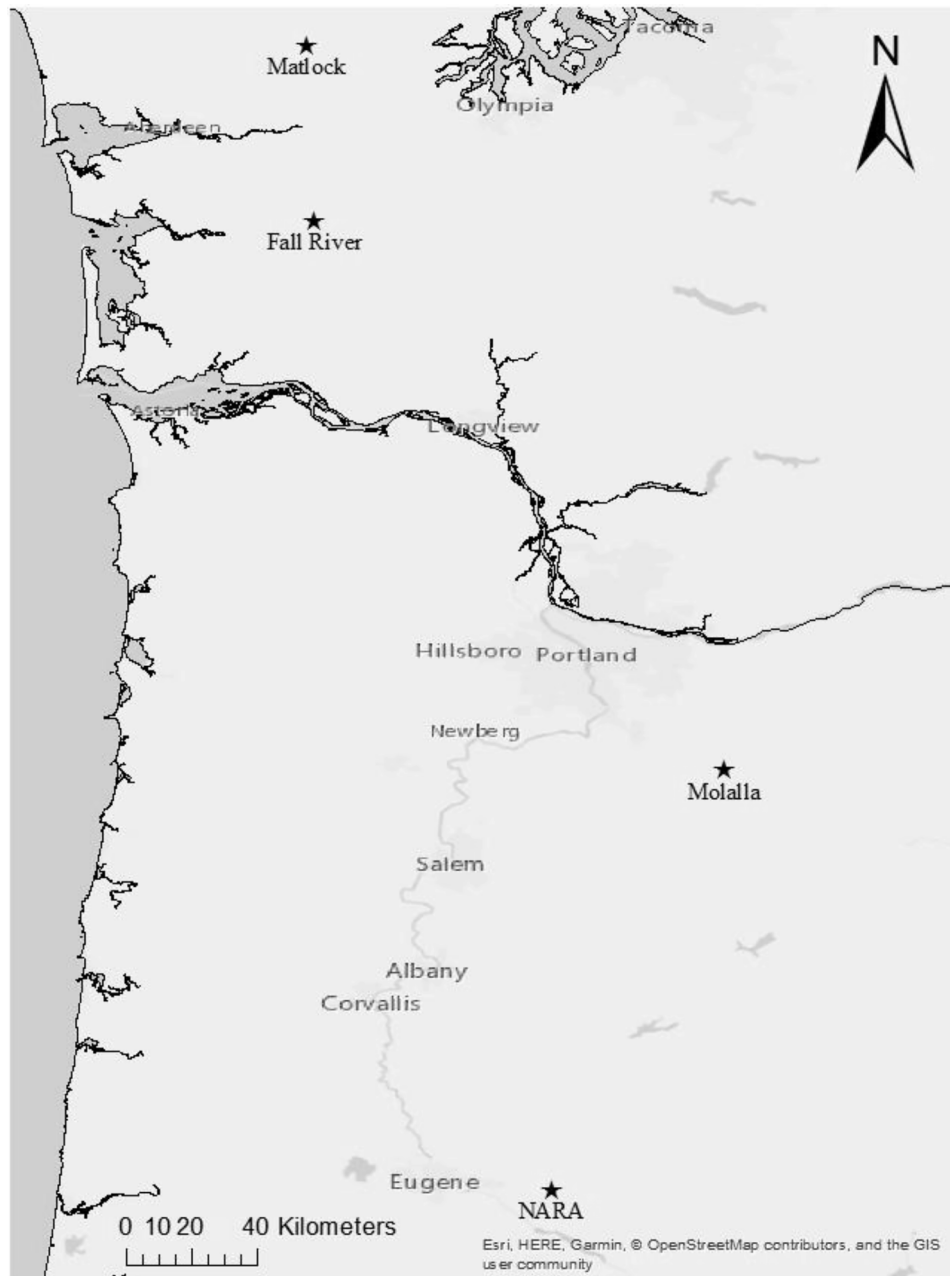


Fig. 1. Long-term Soil Productivity affiliate sites in western Washington and Oregon, USA. Map is sourced from ArcGIS (ArcMap version 10.6, Esri, Redlands, CA).

Table 1
Descriptive site variables and pre-treatment soil data to 1-m depth at the Long-Term Soil Productivity sites in western Oregon and Washington.

Variable	Unit	NARA	Fall River	Matlock	Molalla
Latitude	degrees	44.03	46.72	47.21	45.2
Longitude	degrees	-122.76	-123.42	-123.44	-122.29
Elevation	m	634	334	35	549
Mean Annual Temperature ^a	C	12.2	9.5	10.4	9.8
Mean Annual Precipitation ^a	mm	1,745	2,080	1,884	1,767
Mean Annual Growing Degree Days ^a	Degree Days > 5 °C	2,800	1,931	2,215	2,080
Frost-free Period ^a	days	255	180	204	204
Soil Parent Material ^b	geology	Sedimentary	Basalt	Glacial Outwash	Basic Agglomerate
Geologic Age ^b	period	Oligocene/ Miocene	Miocene	Pleistocene	Miocene
Soil Texture ^b		Cobbly loam –Silty clay loam	Silt loam	Very gravelly loamy sand	Cobbly loam
Available Water Storage (0–100 cm) ^b	cm	17.5	18.3	6.5	19.3
Soil Bulk Density (<2 mm) (0–60 cm)	g cm ³	0.82 ^c	0.75 ^d	0.47 ^e	0.74 ^e
Soil Total N Content (0–60 cm)	kg N ha ⁻¹	7,769 ^c	10,188 ^d	3,300 ^e	7,220 ^e
Soil Exchangeable Ca Content (0–60 cm)	kg Ca ha ⁻¹	5,986 ^c	403 ^d	420 ^e	5,050 ^e
Soil Exchangeable Mg Content (0–60 cm)	kg Mg ha ⁻¹	1,107 ^c	292 ^d	124 ^e	1,430 ^e
Soil Exchangeable K Content (0–60 cm)	kg K ha ⁻¹	1,656 ^c	117 ^d	133 ^e	2,007 ^e
Soil Extractable P Content (0–60 cm)	kg P ha ⁻¹	14 ^c	28 ^d	23 ^e	5 ^e
Previous StandSite Index ^f	m at 50 years	37	42	36	36
Planted Year/ Harvested Year	Year	2013/2014	1999/2000	2003/2004	2003/2004
Planting Density	trees ha ⁻¹	865	1,600	1,111	1,111
Seedling Type		plug + 1	1 + 1	1 + 1	1 + 1
Genetic Gain		2nd generation (gen) Moderate-high	1st gen Low-moderate	1st gen Low-moderate	1st gen Low-moderate

^a Mean annual climate data from Wang et al. (2012) for the five-year period at each site: NARA (2014–2018), Fall River (2000–2004), and Matlock and Molalla (2004–2008);

^b Soil Survey Staff (2019);

^c S. Holub, data not published;

^d Ares et al. 2007;

^e Slesak et al. 2016;

^f King, 1966.

Table 2

Treatments and number of plots at the Long-Term Soil Productivity sites in western Oregon and Washington. Organic matter removal treatments include: bole-only (BO), whole-tree (WT), WT plus coarse woody debris removal (WT+), and WT plus forest floor removal (WTFF). Vegetation control treatments were initial vegetation control (IVC) and five years of annual vegetation control (AVC). All treatments were not compacted except for the compaction (C) treatments.

Treatment combination	NARA			Fall River			Matlock		Molalla	
	IVC	AVC		IVC	AVC		IVC	AVC	IVC	AVC
BO		4	4C	4	4	4C	4	4	4	4
WT		4	4C		4		4	4	4	4
WT+					4					
WTFF		4C								

Table 3

Five-year-old Douglas-fir biomass sampling details at the four LTSP sites including number of samples, mean diameter at 15 cm (D15), mean diameter at breast height (DBH), and mean height (HT) with range in parentheses.

Site	N	Mean D15 (range) (cm)	Mean DBH (range)(cm)	Mean HT (range)(m)	Mean Total Biomass (range)(kg)	Reference
NARA						This study
BO-AVC	4	6.3 (5.3–7.2)	3.1 (2.1–3.5)	3.3 (3.0–3.5)	5.3 (4.2–6.9)	
BO-AVC-C	4	6.8 (5.2–7.5)	3.7 (3.3–4.7)	3.5 (3.2–4.1)	6.3 (3.5–8.6)	
WT-AVC	4	6.6 (5.6–7.9)	3.7 (3.3–4.0)	3.5 (3.2–3.9)	5.7 (4.2–6.4)	
WT-AVC-C	4	6.6 (6.2–7.1)	3.9 (3.6–4.2)	3.4 (3.2–3.6)	5.9 (4.6–6.7)	
WTFF-AVC-C	4	6.5 (5.6–7.3)	3.3 (2.7–3.8)	3.3 (3.0–3.5)	5.9 (4.2–8.8)	
Fall River						Devine et al. (2011)
BO-IVC	24	5.7 (3.7–9.1)	3.6 (2.0–6.0)	3.2 (2.2–4.2)	3.0 (0.9–6.6)	
BO-AVC	20	8.9 (5.3–11.3)	5.0 (2.4–7.0)	3.9 (2.6–5.3)	8.7 (2.7–15.3)	
Matlock						Devine et al. (2011)
BO-IVC	10	3.2 (0.4–5.7)	0.9 (0–2.4)	1.4 (0.4–2.2)	1 (0–2.7)	
WT-IVC	10	2.8 (0.5–4.7)	0.4 (0–2.2)	1.1 (0.4–2.1)	0.8 (0.1–2.2)	
BO-AVC	10	4.7 (0.8–9.5)	2 (0–4.7)	2 (0.3–3.4)	2.7 (0.1–8)	
WT-AVC	10	4.4 (1.2–8.2)	1.5 (0–3.5)	1.7 (0.4–3.3)	2.2 (0.2–6.2)	
Molalla						Devine et al. (2011)
BO-IVC	13	4.8 (2–7.7)	2.3 (0.7–4.2)	2.5 (1.7–3.3)	0.3 (0.3–0.3)	
WT-IVC	14	4.5 (1.2–7.6)	2.0 (0–4.4)	2.3 (0.6–3.6)	0.2 (0.1–0.6)	
BO-AVC	14	4.7 (1.4–9.1)	1.7 (0–4.2)	2.0 (0.6–3.4)	0.1 (0.1–0.1)	
WT-AVC	13	5.4 (0.9–9.6)	2.2 (0–5.7)	2.2 (0.5–4)	0.2 (0–0.5)	

these sites are discussed in more detail in Ares et al. (2007), Harrington and Schoenholtz (2010), and Gallo (2016).

2.2. Soil measurements

Soil samples were taken prior to harvest (NARA, Matlock, and Molalla) or recently after harvest (Fall River) for soil nutrient analysis (Ares et al., 2007; Slesak et al., 2016) (S. Holub, unpublished data) (Table 1). At NARA, pre-treatment soils were sampled for nutrients from 0 to 15, 15–30, and 30–100 cm depths at 25 points within each plot and composited by depth. At Matlock and Molalla, five samples were taken from 0 to 15, 15–30, and 30–60 cm at each plot and composited by depth. At Fall River, one soil pit in a harvested buffer area near each block was sampled by horizon to 150 cm. Total soil N, exchangeable Ca, Mg, K, and Bray P concentrations were converted to nutrient pools from 0 to 60 cm using bulk density and sample or horizon depth (Ares et al., 2007; Slesak, et al., 2016) (S. Holub, personal communication). Soil temperature and soil moisture were measured at each site at 10-cm soil depth five years after planting and averaged by month (Devine and Harrington, 2007; Slesak et al., 2010; Gallo, 2016).

2.3. Individual-Tree Douglas-fir biomass

Douglas-fir biomass sampling at NARA was completed in November 2018. One tree of mean diameter at breast height (DBH) and height (HT) from the buffer of each plot was measured for diameter at 15 cm (D15), DBH, and HT. A total of twenty trees were sampled for biomass at NARA (Table 3). Five-year Douglas-fir tree biomass samples from Fall River ($n = 44$ in February 2005), Matlock ($n = 40$ in February 2009), and Molalla ($n = 54$ in February 2009), which were sampled in a similar method, were also used in this study (Petersen et al., 2008; Devine et al., 2011).

The base of each tree stem was cleared of forest floor and cut at the surface of the mineral soil. The whole tree was removed for subsampling in the lab. Each tree bole was broken into three sections of ~ 1 m to allow for subsampling of foliage, branches, and bole. For each bole section, the branches were separated into small, medium, and large branches and all branch sizes were counted and weighed. A representative number of branches (1–3 branches) from each size class were subsampled and recombined for each bole section. The representative branches were then separated into large branches without needles and branches with needles and subsampled again by weight ratio for each bole section. The subsampled branches were dried at 70° C for two days. Once dry, the branches were stripped of needles by hand and the dry weight of needles and branches were recorded. The percent solids and ratio of dry needle to branch weight was used to estimate the total dry weight of foliage and branches for each bole section and totaled by tree. Bole sections were weighed, and a 2–5 cm stem disk was removed from the bottom of each section. A 2-inch section from the tip of the leader was also sampled from each tree. The stem disk segments were weighed then dried at 70° C until constant mass was attained to obtain percent dry mass. The average percent dry mass from the bottom and top of each bole section was used to estimate the dry weight of each bole section. Bole, branch, and foliage were summed for each tree to determine total biomass.

In August 2018, competing vegetation at NARA was sampled at the mineral soil surface on ten randomly located 0.2 m² subplots from the buffer of each plot. Competing vegetation biomass from all subplots was composited by plot and dried at 70° C for two days. All tree and vegetation samples were individually ground to 2 mm using a Wiley Mill and then finely-ground in a ball mill. Total C and N were measured by dry combustion using a CHN analyzer (CHN 2400, Perkin Elmer Corp.). Competing vegetation biomass and nutrient concentrations at Fall River,

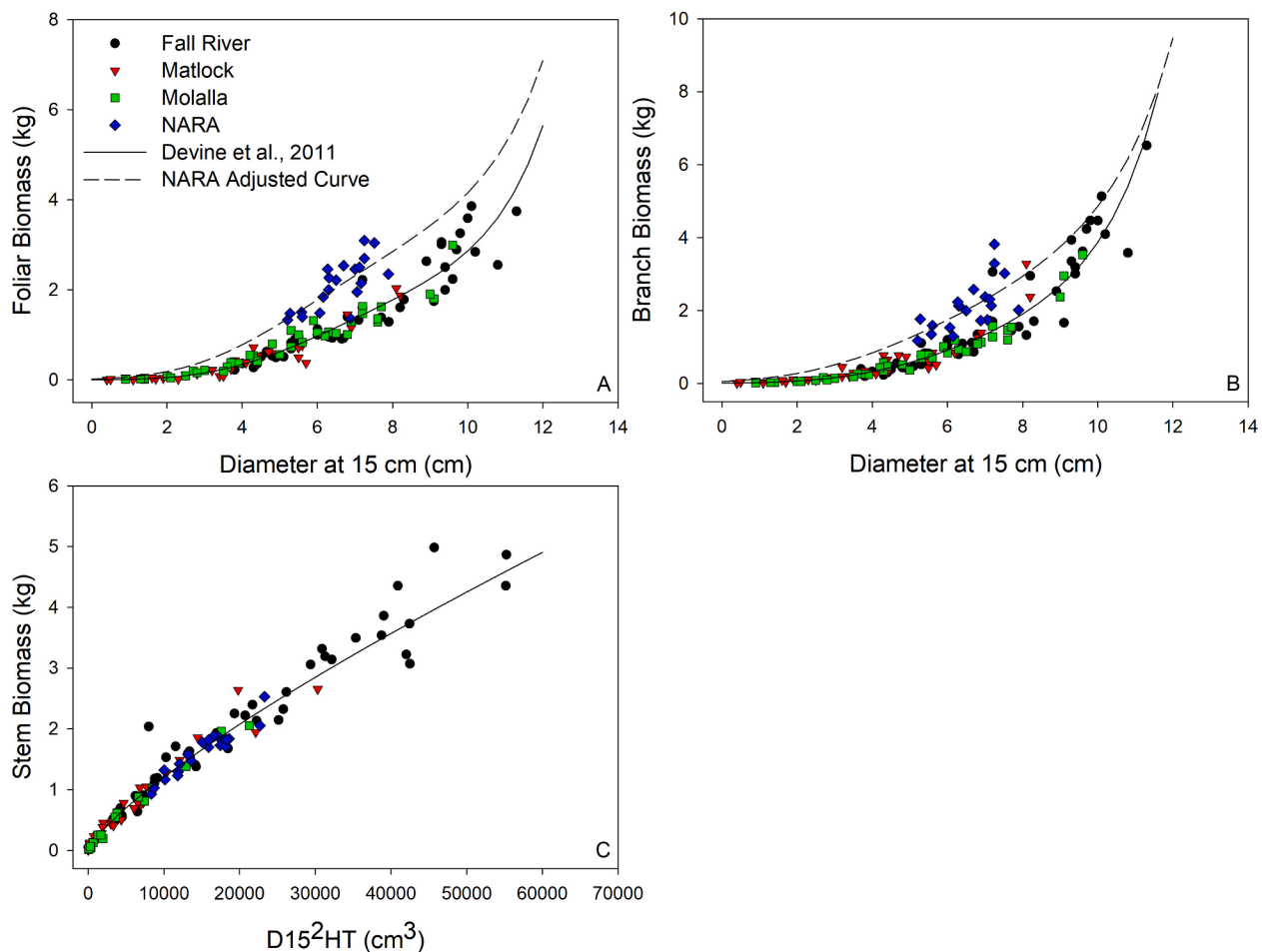


Fig. 2. Individual tree foliar (A) and branch (B) biomass according to diameter at 15 cm (D15), and stem biomass (C) by $D15^2 \cdot \text{height}$ ($D152HT$) with five-year biomass allocation equations from Devine et al. (2011).

Matlock, and Molalla were sampled similarly by Devine et al. (2011).

2.4. Tree measurements

Plot trees were measured for D15 (all trees at planting through 3 years [NARA [175], Fall River [160], and Matlock and Molalla [100]) and a subsample of plot trees at 5 years (NARA [16], Fall River [0], Matlock [78], and Molalla [92]), DBH (trees that had reached DBH), and height. At Fall River, D15 was not measured at 5 years so it was estimated from the relationship between DBH and D15 from 5-year biomass trees at Fall River ($D15_{FR} = 1.4729 \cdot DBH_{FR} + 0.8758$; $R^2 = 0.844$) (W. Devine, personal communication). Periodic growth rates of D15 and height were calculated for the mean of each plot for each measurement period (0–1, 1–2, 2–3, and 3–5 years).

2.5. Individual-Tree biomass allocation equations

Foliar, branch, and stem biomass from all sites were calculated from the biomass allocation equations for 5-year-old Douglas-fir developed from Fall River, Matlock, and Molalla (Devine et al. 2011). Measured biomass at NARA was compared to predicted biomass and adjusted if necessary to improve prediction of foliar, branch, and stem biomass of unmeasured trees. Biomass per ha⁻¹ was calculated as the sum of predicted foliar, branch, and stem biomass per plot size. Total Douglas-fir biomass was calculated as the sum of foliage, branch, and stem biomass per plot.

2.6. Statistical analysis

Data from each site were analyzed separately because of the differences in treatment combinations, planting density, and Douglas-fir productivity. Treatment effects with a blocking factor on periodic D15 and height growth (0–1, 1–2, 2–3, and 3–5 years) at each site were tested using a repeated measures ANOVA. Significant differences were determined using an $\alpha < 0.10$ due to the low amount of replication in this study ($n = 4$). A one-way ANOVA was used to test if treatment combinations of OM removals, vegetation control, and compaction at each site (independent variables: BO-AVC, BO-AVC-C, WT-AVC, WT-AVC-C, and WTFF-AVC-C [NARA], BO-IVC, BO-AVC, BO-AVC-C, WT-AVC, and WT+-AVC [Fall River]), and BO-IVC, BO-AVC, WT-IVC, and WT-AVC [Matlock and Molalla]) with a blocking factor increased five-year Douglas-fir biomass components, competing vegetation biomass, and aboveground N pools (dependent variables). Tukey's honest significance test was used to test significant pairwise comparisons ($\alpha > 0.10$) after ensuring a significant F-test p-value. Site and treatment differences in climate, soil nutrients, soil moisture and temperature (5-year August mean), and foliar and competing vegetation N concentration, biomass, and N pools were visualized using principal component analysis (PCA) for each site and treatment combination. The "prcomp" function in R was used to calculate principal components and the proportion of variance explained by each component (R version 4.0.3., The R Foundation for Statistical Computing). A biplot was graphed using the "ggbiplot" function in the ggplot2 package (Vu 2011).

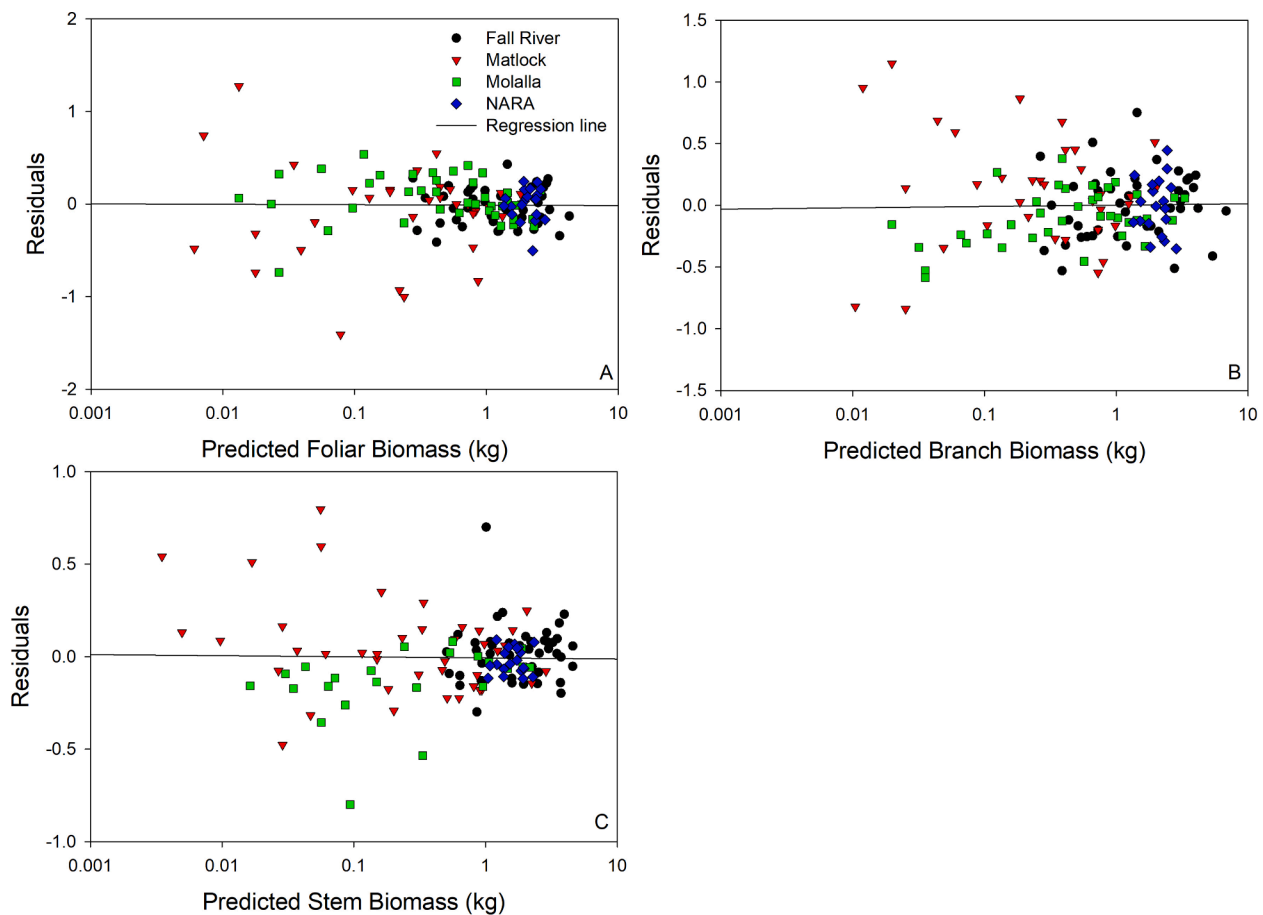


Fig. 3. Residuals for foliar (A), branch (B), and stem (C) biomass.

3. Results

3.1. Individual-tree biomass

Foliar and branch biomass equations developed from five-year-old trees at Fall River, Matlock, and Molalla (Devine et al., 2011) underestimated NARA foliar and branch biomass equations by 3–56% and 9–63%, respectively (Fig. 2A and 2B) (Fig. 2). Predicted foliar and branch biomass at NARA were adjusted using a power equation to better fit measured biomass using the following equations (Figs. 2 and 3).

$$\text{AdjustedFoliarBiomass} = 1.81 * \text{PredictedFoliarBiomass}^{0.79} \quad (1)$$

$$\text{AdjustedBranchBiomass} = 1.86 * \text{PredictedBranchBiomass}^{0.71} \quad (2)$$

In Eqs 1–2, biomass is in kg. Stem biomass at NARA, Fall River, Matlock, and Molalla were adequately predicted by the five-year stem biomass equation from Devine et al. (2011) (Fig. 2C).

3.2. Individual-tree periodic growth rate

At NARA, the BO-AVC treatment had significantly lower D15 and height periodic growth from 0 to 2 years compared to all other treatment combinations (Fig. 4A and 4B). D15 and height growth differences between treatments at NARA decreased over time such that there were no significant differences in D15 and height growth rate between treatments from 3 to 5 years. All treatments at NARA besides the BO-AVC treatment had the greatest 0–3 year periodic D15 growth compared to Fall River, Matlock, and Molalla.

While NARA grew the most in D15 from 0 to 3 years, all Fall River treatments except for BO-IVC had the greatest D15 growth from 3 to 5

years. At Fall River, the BO-IVC treatment had lower periodic D15 growth than the AVC treatments from 1 to 5 years (Fig. 5C). The BO-IVC treatment was also lower in periodic height growth from 2 to 5 years than the BO-AVC and BO-AVC-C treatments (Fig. 5D). In addition, the WT+-AVC treatment had lower height growth than the BO-AVC and BO-AVC-C treatments from 2 to 3 years, yet no significant difference in height growth from 3 to 5 years.

Matlock and Molalla seedlings had the lowest periodic D15 and height growth of all sites from 1 to 5 years (Fig. 4E–H). The BO-AVC and WT-AVC treatments at Matlock grew the most in D15 and height from 1 to 5 years compared to the IVC treatments. All treatments at Matlock experienced a decrease in D15 and height growth from 2 to 3 years compared to 1–2 years. At Molalla, there were no significant treatment effects on D15 growth from 0 to 3 years, but the BO-AVC and WT-AVC treatments had greater D15 growth from 3 to 5 years than the BO-IVC and WT-IVC treatments. While AVC treatments grew the least in height from 1 to 2 years compared to the BO-IVC treatment, there were no significant differences in periodic height growth from 2 to 5 years.

3.3. Aboveground biomass per area

At NARA, treatment combinations including whole-tree removals or soil compaction contained between 958 and 1,333 kg ha⁻¹ greater mean Douglas-fir biomass than the BO-AVC treatment without compaction ($p < 0.001$) (Fig. 5A). Annual vegetation control treatments increased Douglas-fir biomass at Fall River, Matlock, and Molalla over the IVC treatments at 5 years (Fig. 5B–D). Annual vegetation control increased mean Douglas-fir biomass at Fall River (+2,172–4,301 kg ha⁻¹) over the BO-IVC treatment, with the greatest Douglas-fir biomass gains in the BO-AVC and BO-AVC-C treatments ($p < 0.001$) (Fig. 5B). At Matlock, the

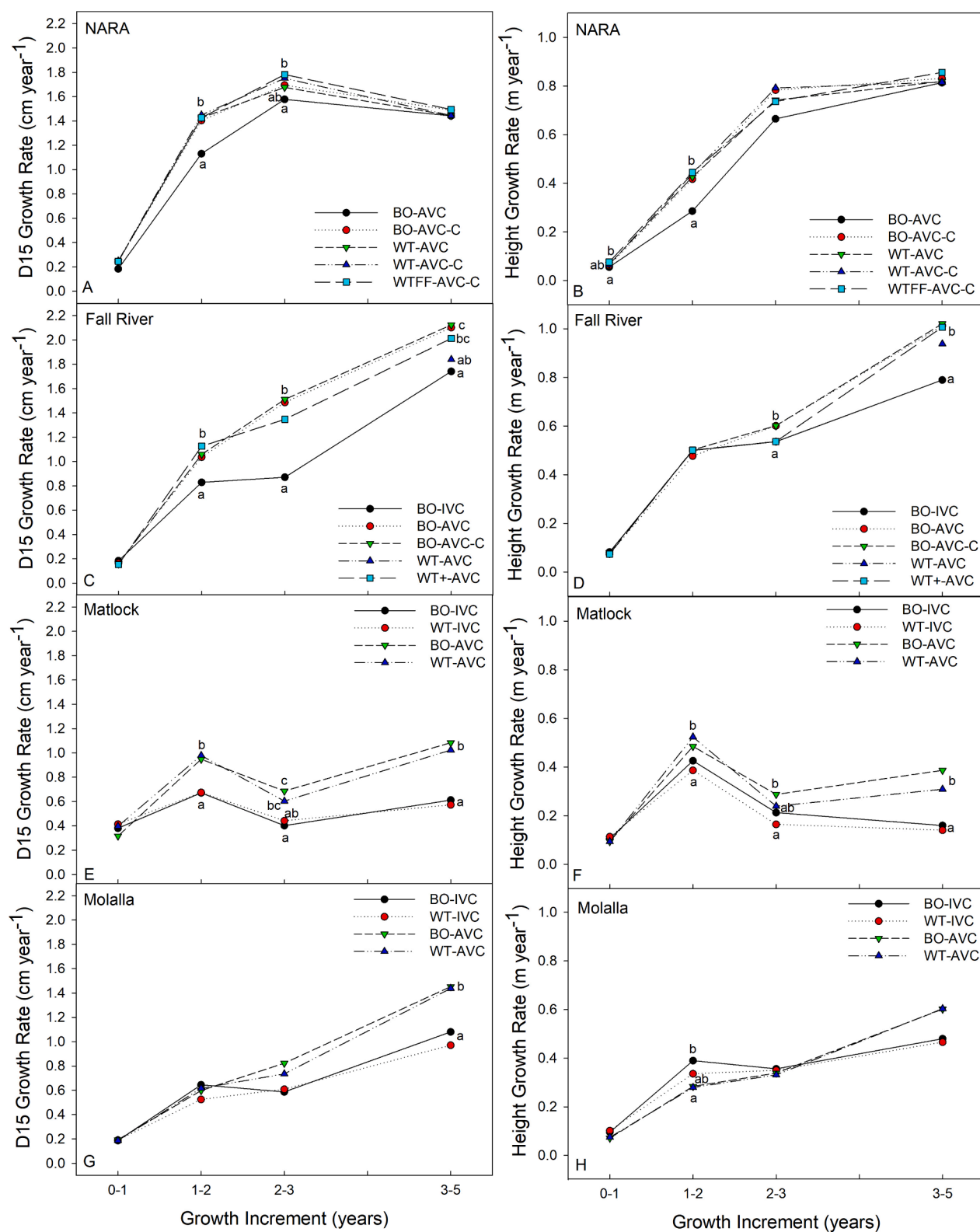


Fig. 4. Average individual-tree periodic diameter at 15 cm (D15) growth rate and height growth rate for each site by treatment combination. Different lowercase letters at each measurement year were significantly different ($p < 0.10$).

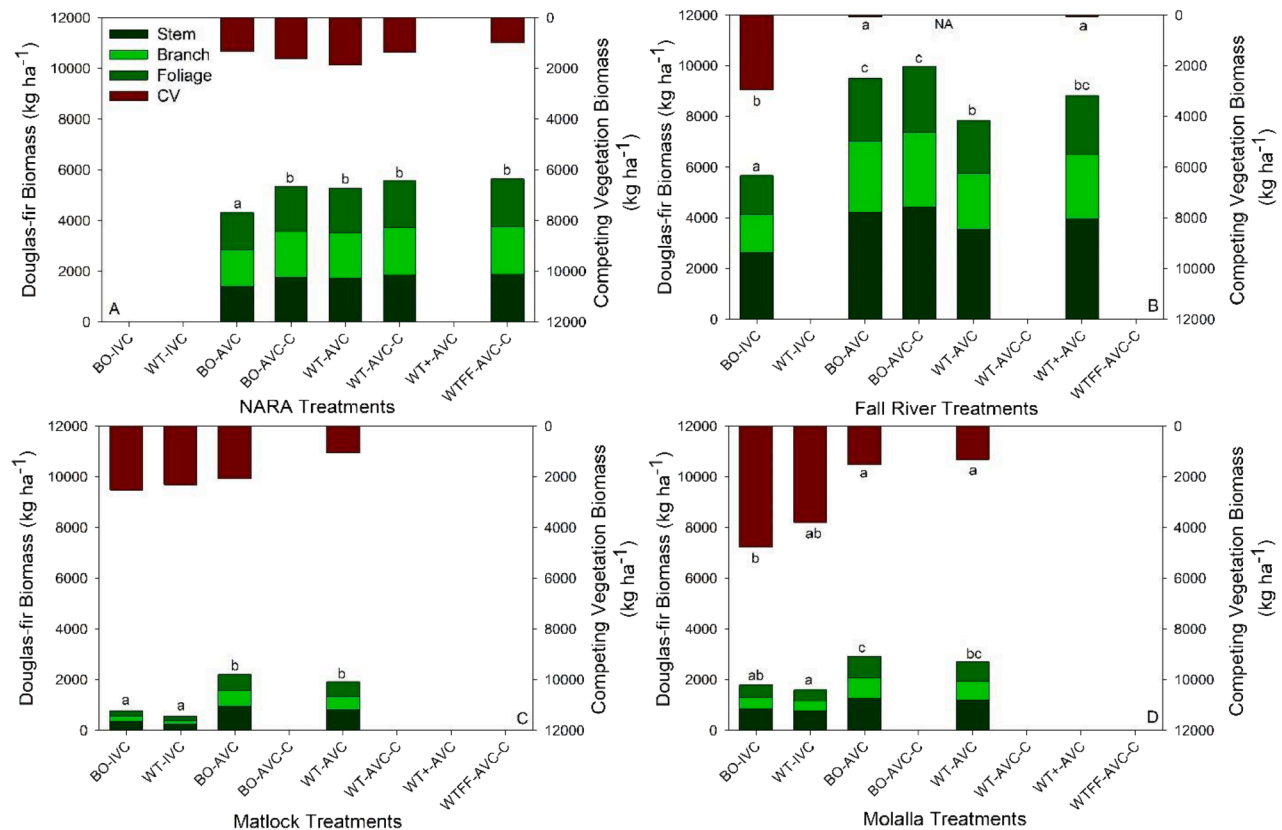


Fig. 5. Per-hectare Douglas-fir foliar, branch, and stem biomass (left/bottom axis) and competing vegetation biomass (right/top axis) for treatment combinations at four LTSP sites five years after treatment: NARA (A), Fall River (B), Matlock (C), and Molalla (D). Planted density was 865, 1,600, 1,111, and 1,111 tree ha⁻¹, respectively, which affects totals. Site treatments with different lowercase letters contain significantly different Douglas-fir biomass ($p < 0.10$). Treatments with no bars were not applied at that site. Competing vegetation was not sampled in the BO-AVC-C and WT-AVC treatments at Fall River.

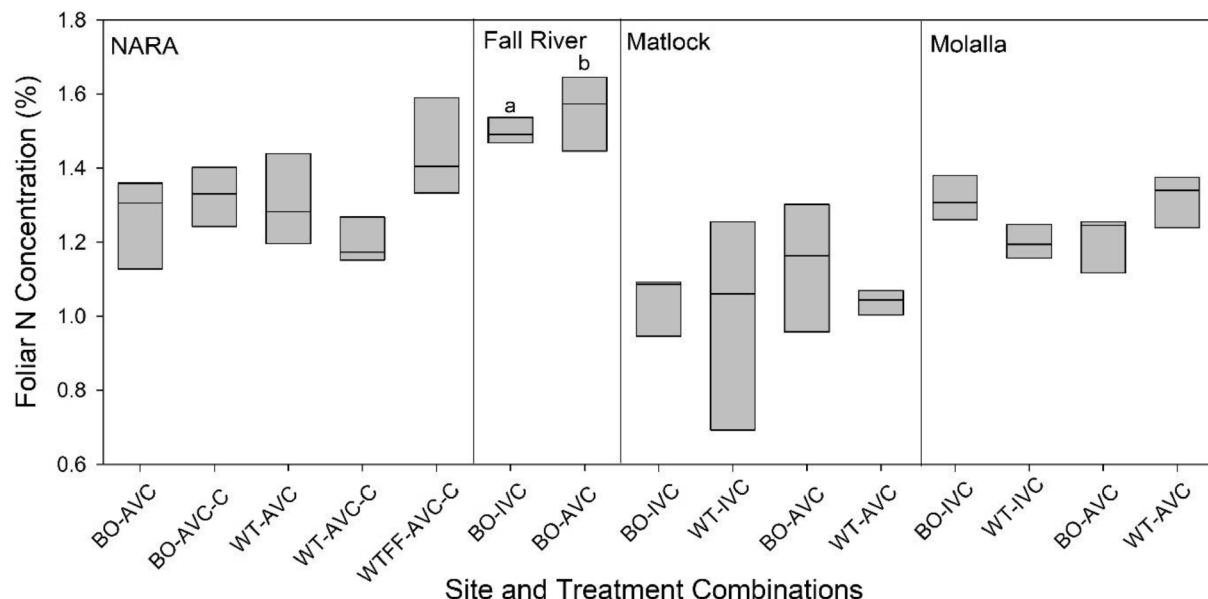


Fig. 6. Foliar N concentration by site and treatment combinations. Treatments within a site with different lowercase letters contain significantly different foliar N concentration ($p < 0.10$).

BO-AVC and WT-AVC treatments contained significantly greater mean Douglas-fir biomass compared to the IVC treatments (+1,239–1525 kg ha⁻¹) ($p < 0.001$) (Fig. 5C). Similar to Matlock, the AVC treatments contained greater Douglas-fir biomass than the IVC treatments (+1,002–1,220 kg ha⁻¹) ($p = 0.02$), but there was no significant

difference between the WT-AVC and BO-IVC treatments (Fig. 5D).

Treatment effects on competing vegetation biomass were variable and site-specific (Fig. 5). At NARA, OM removal and compaction treatments had no significant effect on competing vegetation biomass ($p = 0.30$). The only treatment without AVC at Fall River (BO-IVC) contained

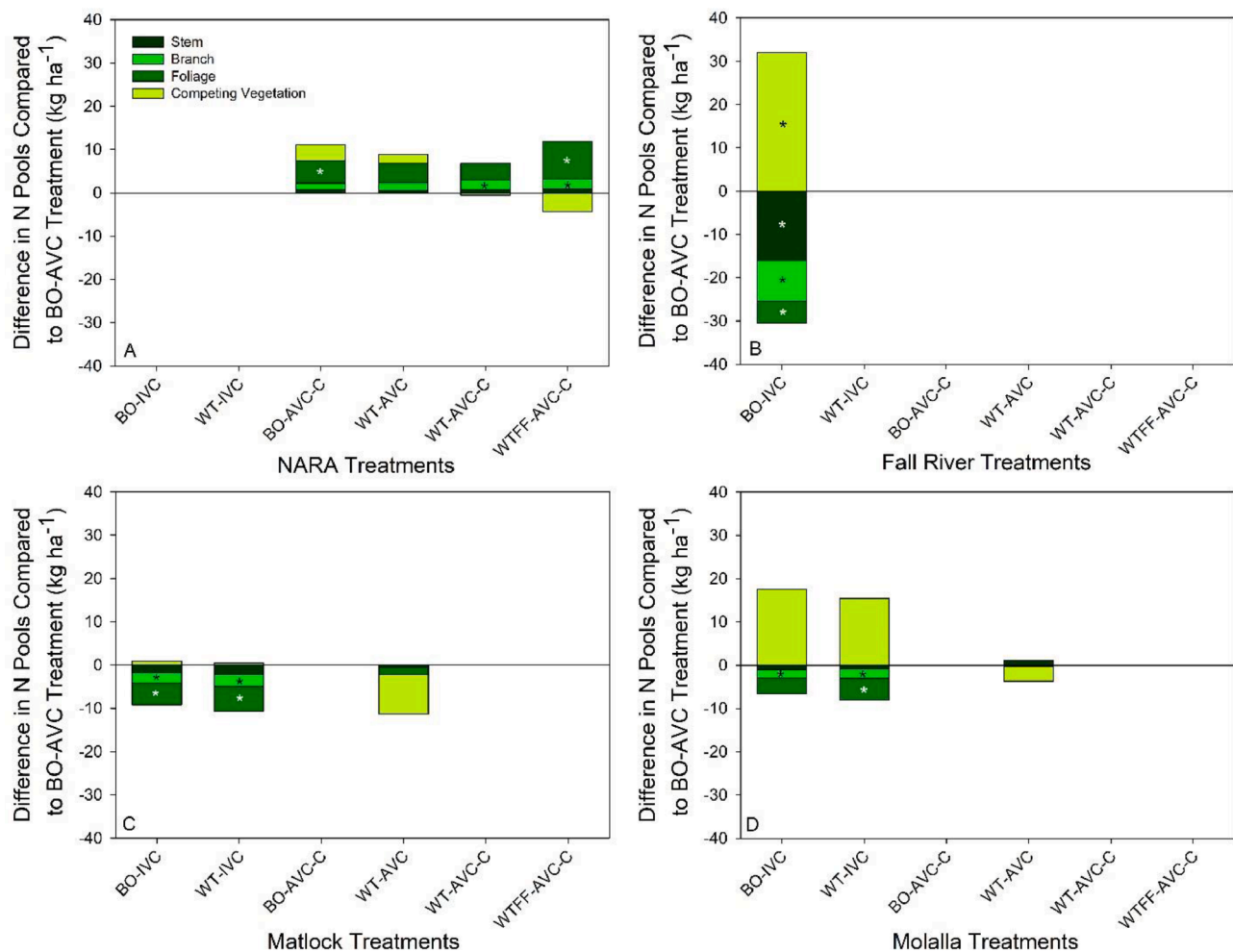


Fig. 7. Net Douglas-fir and competing vegetation nitrogen pools in the whole-tree removal and compaction or annual vegetation control treatments compared to the reference treatment (BO-AVC) at NARA (A), Fall River (B), Matlock (C), and Molalla. Bars with asterisks have significantly different biomass than the BO-AVC treatment ($p < 0.10$).

55–65 times greater competing vegetation biomass than the BO-AVC and WT+AVC treatments (competing vegetation was not measured in the WT-AVC treatment) ($p < 0.001$). At Molalla, greater mean competing vegetation biomass was found in the IVC treatments compared to the AVC treatments (ranging from 2,305–3,466 kg ha⁻¹) ($p = 0.02$). There were no significant treatment effects on competing vegetation biomass at Matlock ($p = 0.26$).

3.4. Foliar N concentration

Foliar N concentrations were highest at Fall River and the NARA WTFF-AVC-C treatment (Fig. 6). At Fall River, the BO-AVC treatment contained significantly greater foliar N than the BO-IVC treatment ($p = 0.09$). The WTFF-AVC-C treatment at NARA was marginally greater than WT-AVC-C treatment and not significantly different than all other treatments ($p = 0.16$). Matlock had the lowest foliar N concentrations compared to the other three sites and there were no significant treatment effects ($p = 0.77$). At Molalla, the BO-IVC and WT-AVC treatments contained marginally greater foliar N concentrations compared to the WT-IVC and BO-AVC treatments ($p = 0.11$).

3.5. Treatment effects on net aboveground nitrogen pools

Douglas-fir and competing vegetation nitrogen pools were significantly affected by OM, vegetation control, and soil compaction treatments. At NARA, Douglas-fir N pools were significantly greater in the

BO-AVC-C and WTFF-AVC-C treatments compared to the BO-AVC treatment mostly due to greater foliar N pools ($p = 0.006$) (Fig. 7A). The BO-IVC and BO-AVC treatments at Fall River contained the same amount of aboveground N pools, but the net increase in the Douglas-fir N pool ($p > 0.001$) was roughly equal to the net loss in competing vegetation N pools ($p < 0.001$) in the BO-AVC treatment (+30 kg N ha⁻¹ versus -32 kg N ha⁻¹, respectively) (Fig. 7B). Annual vegetation control significantly increased Douglas-fir foliar and branch N pools at Matlock in the AVC treatments compared to the IVC treatments ($p = 0.002$ and $p = 0.01$, respectively) (Fig. 7C), but there was no significant effect on competing vegetation N pools ($p = 0.26$). The BO-AVC and WT-AVC treatments also contained greater Douglas-fir N pools than the WT-IVC treatment at Matlock ($p = 0.009$). At Molalla, the IVC treatments contained lower foliar, branch, and total Douglas-fir N pools than the AVC treatments ($p = 0.02$, $p = 0.006$, and $p = 0.007$, respectively) (Fig. 7D). The IVC treatments also contained significantly greater competing vegetation N pools than the WT-AVC treatment ($p = 0.03$).

3.6. Principal component analysis

Results from the PCA indicated that sites and treatments showed clear separation in space among the principal components. The first principal component of the PCA showed a positive relationship between competing vegetation biomass and N pools and fifth growing season summer precipitation and August soil moisture, and a negative relationship with the soil total N pool, foliar N concentration, periodic

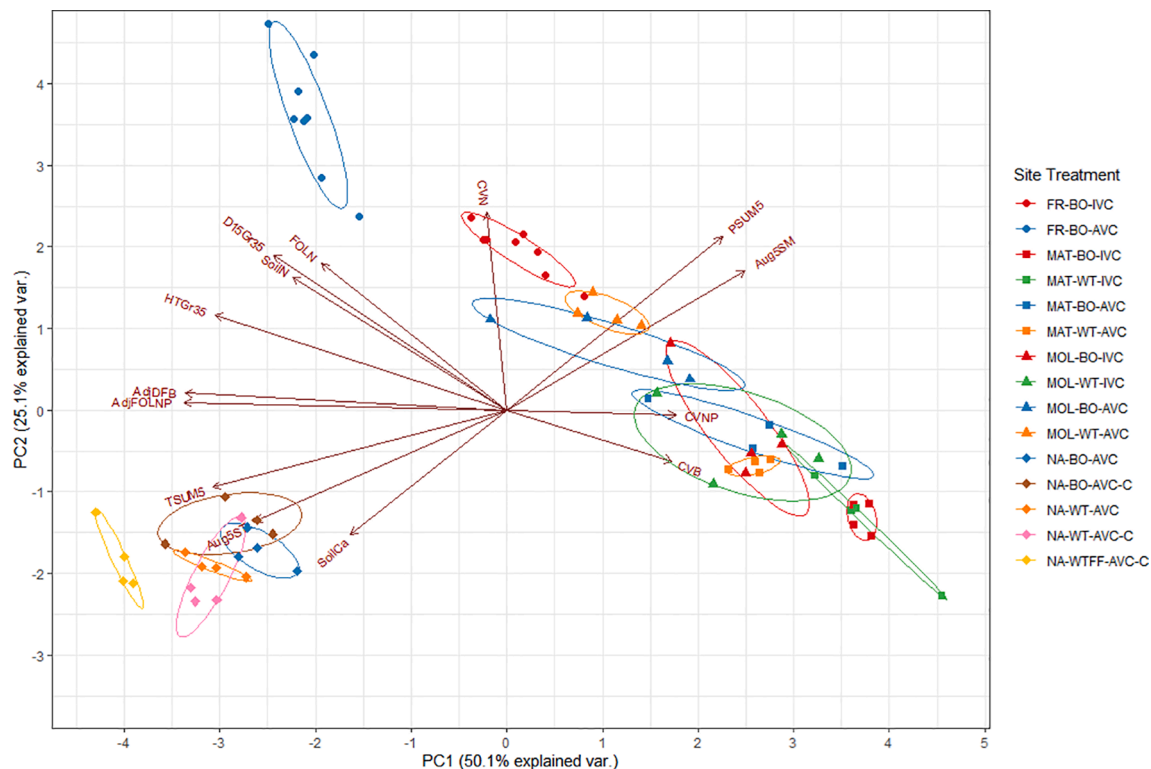


Fig. 8. The first two principal components according to fifth growing season mean annual precipitation and temperature (PSUM5 and TSM5, respectively), fifth growing season August soil temperature and soil moisture (AugST and AugSM, respectively), total soil N (kg ha^{-1}) (SoilN), exchangeable soil Ca (kg ha^{-1}) (SoilCa), foliar and competing vegetation N concentration (FOLN and CVN, respectively), competing vegetation biomass and N pool (CVB and CVNP, respectively), Douglas-fir D15 and height relative growth rate from 3 to 5 years (D15GR35 and HTGR35, respectively), adjusted Douglas-fir biomass (AdjDFB), and adjusted foliar N pool (AdjFOLNP). Site treatment plots are displayed on the principal components with the following abbreviations: Fall River (FR), Matlock (MAT), Molalla (MOL), NARA (NA), initial vegetation control (IVC), annual vegetation control (AVC), bole-only (BO), whole-tree (WT), whole-tree plus forest floor (WTFF), and compacted (C).

height growth from 3 to 5 years, and adjusted Douglas-fir biomass and foliar N pools (adjusted to a planting density of 1,111) (Fig. 8). The soil total N pool, fifth growing season summer precipitation and August soil moisture, competing vegetation N concentration, and periodic D15 growth (3–5 years) were positively associated with the second principal component, while the soil exchangeable Ca pool and fifth growing season August soil temperature were negatively associated.

The NARA treatments were negatively related to the first and second principal components, and the WTFF-AVC-C treatment was separated from the other NARA treatments. The Fall River BO-AVC treatment plots were negatively related to the first principal component and positively related to the second principal component and separated from the Fall River BO-IVC treatment, which was only positively related to the second principal component. The IVC treatments at Matlock and Molalla were more positively related to the first principal component than the AVC treatments.

4. Discussion

4.1. Individual-tree Douglas-fir biomass allocation

Previous research at Fall River, Matlock, and Molalla showed that D15 was the best predictor of individual-tree five-year foliar and branch biomass for all three sites (Devine et al., 2011). However, the first hypothesis was rejected because these biomass equations only accounted for 57–58% of foliar and branch biomass at the NARA site. An improved prediction of foliar and branch at NARA was accomplished through a power equation between predicted and measured biomass. Stem biomass per tree was adequately predicted using the $\text{D15}^2\text{HT}$ equation from Devine et al. (2011) at all four sites, indicating that this equation is broadly applicable across a range of site conditions.

NARA contained twice as much individual-tree foliar biomass at the same D15 than was found at the other three sites. Because NARA was planted at the lowest planting density (50% lower than Fall River and 25% lower than Matlock and Molalla) there was likely greater radiation interception to the whole live crown at NARA (Burkes et al., 2003). Matlock and Molalla also contained a large amount of herbaceous and woody competing vegetation cover relative to planted tree cover (Devine et al., 2011), which would have further reduced Douglas-fir radiation interception. Greater foliar biomass per tree at NARA could also be due to optimal climate and pre-treatment nutrition compared to Fall River, Matlock, and Molalla (Table 1; Figure 9) (Ares et al., 2007; Littke et al., 2020a). While NARA and Molalla contained similar soil nutrients, NARA experienced the warmest mean annual temperatures, greatest growing degree days, and greatest frost-free period of all four sites. Annual and summer precipitation was lowest at the NARA site compared to the other three LTSP yet was only slightly below mean annual precipitation for regional Douglas-fir stands (1,745 mm versus 1,900 mm; Littke et al., 2020a). Another potential reason for increased foliar biomass per tree at NARA is improvements in seedling genetics. The sites established earlier (Fall River, Matlock, and Molalla) were planted with low-moderate genetic gain 1 + 1 seedlings (S. Holub, L. Magalska, and T. Marquardt, personal communications) (Ares et al., 2007; Harrington and Schoenholtz, 2010), while NARA was planted with moderate-high genetic gain plug + 1 seedlings (S. Holub, personal communication). High gain Douglas-fir seedlings have been found to have denser crowns than unimproved and moderate gain Douglas-fir seedlings (du Toit et al., 2020) and higher foliar N (Dwivedi et al., 2019). NARA trees had the highest ratio of foliar biomass to stem biomass (1.5) than Fall River (1.2), Matlock (0.9), and Molalla (0.9) (data not shown), which supports the observation of a denser crown at NARA. Other differences in foliar biomass could be due to different seed

sources at each site. Douglas-fir seed sources from warmer, drier climates with longer frost-free periods (like NARA) typically begin height growth earlier and sustain basal area growth longer than colder and wetter climates (Gould et al., 2012). Over the first five years after planting, the frost-free period at NARA was 51–75 days longer than at Fall River, Matlock, and Molalla (Table 1).

4.2. Douglas-fir growth and biomass per area

Treatment combinations resulted in seedling growth rate differences at each site. Treatment combination effects at NARA were most noticeable in 1–3 year growth. Early increases in growth were likely due to warmer soils in the whole-tree removal treatments and slight increases in soil volumetric water content in the compaction treatments (Gallo, 2016). However, there were no significant differences in D15 and height growth from 3 to 5 years at NARA, which suggests that the early positive effects of whole-tree removals and compaction were wearing off as seedlings became established, treatment effects on microclimate diminished, and the soil recovered from compaction (Page-Dumroese et al., 2006; Thiffault et al., 2011). While soil bulk density was increased one month after compaction, four-year soil samples from NARA showed no significant differences in bulk density between treatments (K. Littke, unpublished data). Early increases in growth, however, resulted in greater five-year Douglas-fir biomass in all treatments compared to the BO-AVC treatment without compaction, which confirms the second hypothesis that OM removal and soil compaction treatment combinations improved Douglas-fir biomass at this site. At Fall River, the BO-AVC-C treatment also had a positive effect on Douglas-fir DBH in year 3 (Ares et al., 2005) and the greatest mean biomass at five years and highest mean volume at ten years (Holub et al., 2013). Similarly, many LTSP studies have found that compaction combined with OM removals resulted in improvements in seedling survival and growth at 5-years (e.g. Fleming et al., 2006) and greater planted tree biomass at 10 years (Ponder et al., 2012). Taken together, findings to date indicate a general benefit of soil compaction to early growth of Douglas-fir in the PNW region on loam to silty clay loam soils. However, the impact of compaction depends upon soil texture and the severity of compaction (Gomez et al., 2002; Page-Dumroese et al., 2006). Decreases in planted tree survival after compaction are also possible due to a reduction in macropores and a higher water table (Simcock et al., 2006).

Annual vegetation control increased Douglas-fir seedling survival while reducing competing vegetation cover at Fall River, Matlock, and Molalla (Roberts et al., 2005; Harrington and Schoenholtz, 2010). Annual vegetation control with or without whole-tree removals increased seedling D15 and height periodic growth rate and Douglas-fir biomass at Fall River, Matlock, and Molalla (Figs. 5 and 7). Furthermore, AVC was associated with increased soil volumetric water content at Fall River, Matlock, and Molalla compared to the IVC treatment (Roberts et al., 2005; Slesak et al., 2010), likely leading to the observed response in growth. These findings are supported by consistently increased growth of seedlings after intensive vegetation control treatments in many forest studies (Fleming et al., 2006). Consistently greater growth with annual vegetation control resulted in larger five-year Douglas-fir biomass and lower competing vegetation biomass (Fig. 8). One exception to this generality occurred at Matlock, where competing vegetation was not significantly affected by vegetation control treatments due to widespread establishment of the invasive Scotch broom (*Cytisus scoparius* (L.) Link) in all treatments (Harrington and Schoenholtz, 2010). Regardless, these findings support the second hypothesis indicating the beneficial effects of sustained vegetation control on early growth across a range of soil fertilities, demonstrating a broad regional effect.

Our results and previous assessments indicate no significant effects of OM removals at NARA, Matlock, and Molalla and variable effects of organic matter removals at Fall River (Harrington and Schoenholtz 2010; Slesak et al. 2010). At Fall River, there was a negative effect of WT-AVC on Douglas-fir biomass compared to BO-AVC, yet this effect

was not seen in the WT+-AVC treatment. The WT-AVC treatment also contained lower D15, DBH, and height than the BO-AVC and WT+-AVC treatments at age 5. The WT+-AVC treatment likely resulted in greater growth over the WT-AVC treatment due to increased net mineralization rates after planting due to warmer soil temperatures (Smethurst and Nambiar, 1990; Licata 2004; Roberts et al. 2005; Devine and Harrington, 2007). However, early growth of seedlings at Fall River was highly related to soil moisture and the BO-AVC treatment had greater growth during drier years (O'Connell et al., 2004; Roberts et al. 2005). Except for the WT-AVC treatment at Fall River, it appears that OM removal has a limited effect on early performance of planted Douglas-fir across a wide range of site conditions and climate in the region. Similar to the results from these four sites, in a meta-analysis Thiffault et al. (2011) found no consistent effect of OM removal on seedling survival and growth.

4.3. Aboveground nitrogen pools

The BO-AVC-C and WTFF-AVC-C treatments at NARA resulted in the greatest Douglas-fir N pools mostly due to greater foliar N pools. At NARA, there were no significant differences in Douglas-fir component N concentrations between treatments, therefore, the changes in Douglas-fir N pools were due to greater growth and biomass in these treatments. Similarly, previous research has shown little effect of compaction and organic matter removals on seedling foliar N except for one interior Douglas-fir site (Ponder et al., 2012). Because vegetation was controlled in the same manner on each treatment at NARA, there were no differences in competing vegetation N pools. Blocks at NARA were defined by pre-planting total soil nitrogen content and there was a growth response difference among plots with the higher N block tending to have increased growth relative to lower N blocks (S. Holub, personal communication). This aligns with results from Devine et al. (2011) who found that Douglas-fir and competing vegetation N pools were strongly related to soil pools.

Whole-tree removal treatments did not affect Douglas-fir N pools on all four sites. Five years of annual vegetation control tended to increase Douglas-fir N pools due to changes in aboveground biomass while decreasing competing vegetation N pools. The only change in N concentration was at Fall River where stem and branch N concentrations were greater in the BO-IVC treatment and foliar N concentration was greater in the BO-AVC treatment (Petersen et al. 2008). At Fall River, the increase in the Douglas-fir N pool in the BO-AVC treatment was equal to the increase in competing vegetation N in the BO-IVC treatment such that both treatments contained the same aboveground N pool, which suggests that increased available N following AVC was fully utilized by the Douglas-fir seedlings. At Matlock and Molalla, there was a larger decrease in competing vegetation N pools than the increase in Douglas-fir N pools, indicating that some of the increased available N following AVC was leached or incorporated into soil pools (Slesak et al. 2016). However, changes in total aboveground N pools were not significant at these sites. The use of sustained vegetation control shifted the aboveground N pool from competing vegetation to Douglas-fir.

4.4. Factors influencing site level responses

Results from the PCA indicated that sites (and to a lesser extent, treatments within a site) clearly separated within the space defined by principal components 1 and 2. Patterns in response may provide insight into key factors that govern the general growth responses within each of the sites. For example, Matlock plots were found to be positively related to the first principal component, which was associated with greater competing vegetation and vegetation control. The glacial outwash soil at Matlock has low water holding capacity and nutrient pools (Table 1), and competition for limited resources likely caused a disproportionate effect on growth. At the Molalla site, competing vegetation and vegetation control was also important, but climate had a large influence and

may be more limiting to growth given the higher soil fertility at that site relative to Matlock. At Fall River, which has the highest soil total N pools and available water holding capacity of these sites, annual vegetation control, faster growth rates, and greater nutrient availability resulted in the greatest Douglas-fir biomass and N pools compared to all other sites. Similar to Fall River, NARA contained high soil N and high Douglas-fir biomass and N pools yet differed from Fall River due to high soil exchangeable cation pools and warmer air and soil temperatures. The general patterns of the principal component analysis support the third hypothesis that responses in Douglas-fir growth and biomass to vegetation control, organic matter removal, and compaction are dependent on local limitations in climate, soil nutrition, and competing vegetation severity.

5. Conclusions

Foliar and branch biomass equations from Devine et al. (2011) underpredicted biomass at the NARA site, which could be due to a lower planting density, a warmer climate, improvements in seedling genetics, and different seed sources at that site. However, stem biomass was accurately predicted using the previously published D15²HT equation (Devine et al. 2011), indicating broad applicability across a range of site conditions.

Whole-tree and soil compaction treatment combinations at NARA increased Douglas-fir D15 and height growth from 1 to 3 years and five-year Douglas-fir biomass. Annual vegetation control improved Douglas-fir growth and biomass at most sites due to improvements in water and nutrient availability. The greatest effect of these treatments in periodic D15 and height growth was found in years 1–5. Whole-tree removal treatments had no significant effect on foliar, branch, stem, and total Douglas-fir biomass at most sites except for Fall River where the WT-AVC treatment underperformed compared to the BO-AVC and WT+AVC treatments. These findings suggest that sustained vegetation control has the largest positive effect on Douglas-fir growth and biomass.

According to the principal component analysis, Douglas-fir growth and biomass at these four sites were positively related to warmer climate and greater N availability and negatively related to summer precipitation, August soil moisture, and competing vegetation biomass and N pools. Annual vegetation control treatments resulted in the greatest differences in within-site Douglas-fir growth, biomass, and N pools and were affected by the considerable differences in climate, soil nutrition, and competing vegetation biomass between sites.

CRedit authorship contribution statement

K.M. Littke: Conceptualization, Data curation, Methodology, Formal analysis, Investigation, Validation, Writing - original draft, Writing - review & editing, Visualization. **S.M. Holub:** Formal analysis, Writing - original draft, Writing - review & editing. **R.A. Slesak:** Formal analysis, Writing - original draft, Writing - review & editing. **W.R. Littke:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **E.C. Turnblom:** Project administration, Funding acquisition, Formal analysis, Resources, Supervision, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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