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Long-term effects of tree spacing during reforestation on survival and growth of three important tree species in the Pacific Northwest, USA

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ABSTRACT

Tree spacing during reforestation is a critical decision that influences the trajectory and rate of stand development over time, but there is limited quantification of responses at meaningful time scales for management. Here we report on ~40 year response of coast Douglas-fir (DF, *Pseudotsuga menziesii* var. *menziesii*), noble fir (NF, *Abies procera*) and western white pine (WWP, *Pinus monticola*) to five or six spacing treatments that ranged from 1 to 6 m in the western Cascades of Washington, USA. Spacing effects were tested separately for each species in completely randomized designs applied to 0.4 ha plots with 4–6 replications per treatment. There was no effect of spacing on relative survival in WWP and NF; for DF, relative survival decreased with decreasing spacing, with the effect becoming more pronounced with time. Quadratic mean diameter generally increased with increasing spacing for WWP and DF, but the effect attenuated at 4-m spacing and higher. Total stand volume was inversely related to spacing for all species for much of the study period, but there was no difference in volume among spacings for DF in the most recent measurement because of the density-dependent mortality in narrow spacings as Stand Density Index increased above 55 % of maximum. Our findings indicate that wider spacings (5–6-m) promote the development of larger trees with more complex stand structure (including that arising from ingrowth), while spacings of 3–4-m will maximize wood production. The implications of these findings are discussed in the context of management objectives, silvicultural resource constraints, and species-specific considerations.

1. Introduction

Decisions on what and how to plant during reforestation influence the success of short-term stand establishment and longer-term forest development and function. Such decisions are critically important as they influence the trajectory of stand development and eventual capacity to meet management objectives such as resiliency to changing climate or sustainable production of wood and other forest products (Dobrowski et al., 2024, Rubilar et al., 2018). Tree spacing at time of planting is one critical decision as it influences the ability of planted trees to acquire resources needed for survival and growth (Oliver and Larson, 1996), ultimately driving differences in stand-level structural characteristics as development proceeds from young, open-canopied conditions (Scott et al., 1998) through canopy closure and beyond (Harrington et al., 2009, Gabria et al., 2023). Resource acquisition of any individual tree is influenced by competition with other trees (which increases with decreasing spacing or increasing density) as well as other vegetation that becomes established prior to or after planting occurs (Oliver 1990, Wagner et al., 1999); because of this, competition for resources is generally high during the establishment phase regardless of planting density (Balandier et al., 2006). Total stand volume growth in this early stage of development is generally greatest in stands planted at a narrow spacing (high density) compared to wider spacings as more growth resources are captured by planted trees (Harrington et al., 2009, Scott et al., 1998). At later stages of development, higher planting densities eventually succumb to competition-induced mortality, resulting in lower total stand growth compared to stands initially planted at lower densities where individual (and total stand) growth remain high (i.e., the “crossover” effect, *sensu* Oliver and Larson, 1996).

Given the importance of initial tree spacing to stand development and productivity, several studies have investigated its effect on early survival and growth in forests of the Pacific Northwest (PNW) USA (Reukema, 1979, Scott et al., 1998, Woodruff et al., 2002, Harrington et al., 2009). An underlying objective of past work was to determine

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which tree spacing, either alone or in combination with other management activities such as forest thinning, would maximize stand productivity and economic return over a given rotation. Currently, production-oriented coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) sites west of the Cascade crest are commonly planted at a spacing of 3 m which has been shown to balance diameter and volume growth up to age 25 (Harrington et al., 2009). Stands planted at this density are commonly precommercial thinned in the second decade after planting to redistribute limited site resources to dominant and codominant trees. In the absence of thinning at this density, tree to tree resource competition will increase over time, slowing or stagnating stand growth as competition-induced mortality occurs (Curtis, 2006).

Lower planting densities (wider spacing) than typical for production systems may be more appropriate for different management objectives or in response to changing economic and environmental conditions (Dobrowski et al., 2024, Rubilar et al., 2018). For example, North et al. (2019) outlined substantial reductions in forest thinning actions on USFS National Forest System (NFS) lands which were attributed to limitations in workforce and funding availability. Because of this, managers may choose to plant at lower densities to avoid the need for thinning in the future. At the same time, the amount of NFS land requiring reforestation has drastically increased in response to catastrophic wildfires across the western US (USDA Forest Service, 2022) while nursery capacity has decreased (Dobrowski et al., 2024, Fargione et al., 2021). In response, NFS managers may plant at lower densities (<200 trees per acre) to increase the amount of land area that can be planted in a given year with limited seedlings. Lower stand densities, either via initial planting or thinning, also have potential to increase forest resilience to extreme conditions such as drought (North et al., 2022) and promote the development of forest structure important for wildlife habitat (Dodson et al., 2012, Sullivan et al., 2001).

Most spacing studies in the PNW region have evaluated short-term responses for only a few commercially dominant species (e.g., Douglas-fir, <10 years; Scott et al., 1998, Woodruff et al., 2002, Harrington et al., 2009), and do not address current information needs associated with changing management objectives and environmental conditions. There are limited reports of long-term responses to spacing treatments that may inform managers who are considering lower planting densities than typically used in production forestry. In situations where thinning (precommercial or commercial) is not planned for the stand, quantifying the longer-term response is critical as tree-to-tree competition and its effects increase with time and in response to extreme weather events associated with climate change (D'Amato et al., 2013).

A series of spacing trials were established between 1980 and 1982 at the Wind River Experimental Forest in the Western Cascades of Washington, USA. The trials tested five or six spacing treatments from 1 to 6 m that were applied to three tree species that are economically and ecologically important in the PNW region: Douglas-fir, noble fir (*Abies procera*) and western white pine (*Pinus monticola*). Previous reports between 16 and 33 years after planting documented limited effects of spacing treatments on tree height variables, but a significant increase in individual tree diameter growth and decrease in total stand volume with increasing spacing (Harrington et al., 2009, Curtis et al., 2016, Bishaw et al., 2003, Curtis et al., 2013). Here we report growth responses of these species ~40 years after planting, and also report spacing effects on understory vegetation composition in the Douglas-fir plots only. Our objective was to determine how species and spacing at time of planting influence long-term tree survival, growth, understory plant communities, and stand structure over a period that approximates a typical rotation length in the region.

2. Methods

2.1. Study site description

The trials are located in the Trout Creek Division of the Wind River Experimental Forest, Washington USA (45.828 ºN, −121.997 ºE). The regional climate is Mediterranean with cold, moist winters, and dry summers with prolonged periods of drought. Mean annual temperature at the site is 8.7°C (15.2°C during May-Sept) and annual precipitation is 2510 mm (270 mm falling during May-Sept) (monthly normals 1991–2020, PRISM Climate Group). Soils developed as residuum from basalt and are classified as a medial, amorphic, mesic vitric hapludand with a loam texture (Stabler series; Soil Survey Staff, 2024). Elevation at the sites range from 500 to 860 m with slopes of ~10 % across most of the site, but with some portions (those used for the noble fir trial – see below) much steeper (~70 %). The pre-harvest old-growth stand was dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*) with minor components of Pacific silver fir (*Abies amabilis*), western redcedar (*Thuja plicata*), and noble fir; the understory was composed of vine maple (*Acer circinatum*), Pacific dogwood (*Cornus nuttallii*), salal (*Gaultheria shallon*), Oregon grape (*Mahonia aquifolium*), and beargrass (*Xerophyllum tenax*), among other minor species (Bishaw et al., 2003). The site was clearcut in 1977, slash burned in 1978, and then planted between 1979 and 1981 depending on species (see details below).

2.2. Experimental design and measurements

Each species was installed as a separate experiment but with similar spacing treatments among them. The overall design for all species was a completely randomized design with spacing treatments: for noble fir (NF) and western white pine (WWP), spacing treatments included, 2-, 3-, 4-, 5-, and 6-m spacings; for Douglas-fir (DF), spacing treatments included 1-, 2-, 3-, 4-, 5-, and 6-m spacings. All treatments were applied to square plots 0.4 ha in size, but replication was variable depending on spacing and species (Supplemental Figure S1). WWP spacings of 2-, 4-, 5-, 6-m were each replicated three times and the 3-m spacing was replicated six times; all NF spacing treatments were replicated four times; DF spacings of 2-, 3-, 4-, 5-, and 6-m were each replicated six times and the 1-m spacing was replicated four times. The variation in the number of replicates was primarily due to financial and logistical constraints, notably for the 1-m spacing treatment (limited seedlings were available for WWP and NF). The number of trees planted at 1-, 2-, 3-, 4-, 5-, and 6-m spacings was 10,000, 2500, 1111, 625, 400, and 278 trees per hectare (TPH). In all instances, individual planting locations were delineated and marked to ensure that the target spacing was uniformly achieved. Bareroot 2–0 seedlings were planted for NF in Spring of 1980, for DF in Spring of 1981, and for WWP in Spring of 1982. Seed sources were from a local population at elevation of 610 m for DF, and a local population at 915 m for NF. For WWP, the species is highly susceptible to white pine blister rust (*Cronartium ribicola*); seed was sourced from blister rust-resistant mother trees from an elevation of 760–1070 m (Bishaw et al., 2003).Additional actions were taken to ensure that the treatment spacing was maintained including competition control via herbicide application in the first year after planting, replacement of dead planted trees for the first 3 years after initial planting, and periodic removal of volunteer seedlings/trees via cutting. Ten of the NF plots had *Ceanothus velutinous* annually removed within 1 m of planted seedlings in 1990 (Erickson and Harrington, 2006). More details on treatment application specific to each species are available in Curtis et al., 2013, Harrington et al., (2009), and Bishaw et al., 2003.

Measurements were conducted on tagged trees located in permanent plots that were established in 1989 (7–9 years after planting). Measurement plots were variable in size depending on the spacing treatment but consistent across species: the number of tagged measurement trees per plot was 200 for the 1- and 2-m spacings (arranged as two 100-tree plots within the treatment plot), and 196, 100, 64, and 49 trees for the 3-, 4-, 5-, and 6-m spacings, respectively. Periodic measurements were initiated in 1989 and varied across species, but we focus on the following measurement periods for this analysis: DF was measured in 1997, 2001, 2005, 2013, and 2021 (40 years after planting); NF was measured in 1997, 2001, 2005, 2009, 2013, and 2021 (41 years after planting); WWP was measured in 1997, 2002, and 2021 (39 years after planting). Measurements occurred after growth cessation in the associated year; trees were recorded as alive or dead, all live trees were measured for diameter at breast height (DBH; precision of 0.1 cm), and a subset of trees (~40–60 per plot) were measured for total height and height to live crown (precision of 0.1 m). Ingrowth was tagged and measured on all trees > 4 cm DBH throughout the study period.

Understory vegetation was measured at all DF plots in July 2021 to assess treatment effects on understory composition. A fixed 5.64-m radius circular plot was established at the approximate center of the measurement plot in each treatment plot. Cover of all herbaceous plants, shrubs, and trees (i.e., canopy cover) were visually estimated by height class to the nearest 1 % for cover estimates between 1 % and 10 % and the nearest 5 % for cover estimates > 10 %. Herbaceous species < 1 % cover were not recorded except for non-native species and graminoids. Tree regeneration (> 5 cm height and <5 cm DBH) counts were measured in a nested 2-m radius plot by tree species and 1-cm size classes.

2.3. Data analysis

Each species was analyzed independently for all analyses. We calculated plot means for each species and measurement period for the following variables: relative survival (as a proportion) of originally planted trees, quadratic mean diameter (cm), mean total height and height to live crown for trees measured for height only (m), total live basal area (m^2 ha^{-1}), total wood volume (m^3 ha^{-1}), and Reineke's Stand Density Index (SDI, Reineke, 1933). We also calculated live tree density (TPH) for each treatment at the last measurement period to account for ingrowth over the study period. For total wood volume estimates, we first estimated the height of trees only measured for DBH using linear regression height-diameter models developed from measured height trees for each species by spacing treatment. Individual tree volumes were then calculated using published equations for DF (Bruce and DeMars, 1974), NF (Browne, 1962), and WWP (Wykoff et al., 1982) (see equations in Supplemental Materials Table S1), which were then summed within a measurement plot to estimate total volume per ha. For understory data collected in the DF plots only, we summed percent cover estimates for a given species across height classes, and then summed within herbaceous, shrub, and tree classes prior to analysis.

We fit species-specific generalized linear mixed models to assess spacing treatment effects over the entire study period for each of the following plot-level response variables: relative survival, quadratic mean diameter, total wood volume, SDI, and live basal area. For each species and response variable, we fit a model that included the fixed categorical predictors of spacing, stand age, and a spacing by stand age interaction term and a random effect of plot to account for repeated measures over time. Models were fit with a gamma distribution except models of relative survival, which were fit with a binomial distribution. We then assessed spacing treatment effects for just the most recent measurement in 2021 (stand ages of 39–41 years) using species-specific generalized linear models for the following plot-level response variables: live tree density, total height, height to live crown, proportion cover of herbaceous, shrub, tree regeneration and overstory trees, and herbaceous, shrub, and total species richness (cover and richness response variables for DF only). For each species and response variable, we fit a model that included spacing as a single categorical predictor. Models of live tree density were fit with a negative binomial distribution, models of height and richness response variables were fit with a Gaussian distribution, and models of proportion cover response variables were fit with a beta distribution.

Statistical analyses were conducted in R version 4.4.0 (R Core Team 2024). Models were fit with glmmTMB (Brooks et al., 2017) and were evaluated with DHARMa (Hartig 2021). Model evaluation included evaluation for outliers and uniform residuals prior to interpretation. We used and alpha level of 0.05 to determine significance of model predictors. If spacing and/or the interaction term (in repeated measures models) was significant, we performed pairwise comparisons between all spacing treatments within each measurement period using Tukey's honestly significant difference (HSD) test in emmeans (Lenth 2024). Results were visualized with ggplot2 (Wickham 2016) and patchwork (Pedersen 2024).

3. Results

3.1. Survival and ingrowth

There was no effect of spacing on relative survival for WWP or NF, but there was an effect of spacing for DF that varied with time ($p < 0.001$; Fig. 1, Supplemental materials Table S2). For DF, effects generally manifested as decreasing relative survival with decreasing spacing, where the 1- and 2-m spacing treatments had notable reductions in survival rates with time (Fig. 1). By the end of the study period, relative survival in the 1- and 2-m spacings was significantly lower than in all other spacing treatments, and relative survival in the 3-m spacing (0.68, 95 % CI: 0.60–0.74) was significantly lower than in the 6-m spacing (0.90, 95 % CI: 0.83–0.94) but not different from the 4-m (0.81, 95 % CI: 0.74–0.87) or 5-m (0.83, 95 % CI: 0.75–0.89) spacing. Overall survival was lowest for WWP by the end of the study period (average of 0.50 across all spacing treatments; Supplemental Table S3). Relative survival for NF at the end of the study period ranged from 0.52 (95 % CI: 0.32–0.71) in the 2-m spacing to 0.75 (95 % CI: 0.57–0.88) in the 6-m spacing, with an average relative survival of 0.64 across all spacing treatments (Supplemental Table S4).

Live tree density (planted + ingrowth) at the end of study period varied with spacing treatment for all species (Supplemental Table S2). NF had notable increases in density above the planting density for spacings of 3–6 m; this same response (i.e., net recruitment) was observed at 6-m spacing in WWP, and 5- and 6-m spacing in DF (Table 1). Recruitment composition was dominated by DF across all species treatments and most spacings, followed by western hemlock. DF and western hemlock recruitment were inversely proportional across spacing treatments in the DF treatment blocks, with relative western hemlock recruitment increasing with increasing spacing (data not shown).

3.2. Growth responses

Spacing treatment had a significant effect on quadratic mean diameter (QMD) that varied with time for all species ($p < 0.001$, Supplemental Table S2), but pairwise comparisons failed to detect significant differences between spacing treatments within a measurement period for NF, due to high within-treatment variability (Supplemental Table S4). For WWP and DF, QMD increased with increasing spacing, but differences attenuated at 4-m spacing and higher. This pattern remained similar in each measurement period despite the significant interaction between spacing and stand age (Fig. 2). Average QMD in the 4–6-m spacings at the end of the study period was approximately 31.6, 25.0, and 31.3 cm for WWP, NF, and DF, respectively (see Supplemental Tables S3–5 for treatment means and confidence intervals for each spacing and species).

There was no effect of spacing treatment on total height for either WWP or NF by the end of the study period ($p > 0.3$); height tended to increase from 1 to 3-m spacing in WWP but there was no discernable pattern in NF which was associated with high variability (Fig. 3). In contrast, there was a significant effect ($p = 0.002$) of spacing treatment on total height for DF which manifested as significantly lower height in the 1-m spacing compared to spacings 3-m and greater (Fig. 3). The response of height to live crown (HLC) was opposite to that of total height, where HLC generally decreased with increasing spacing (Fig. 3). For WWP, HLC was significantly greater in the 2-m than the 5- and 6-m spacings. For DF, HLC was significantly greater in the 2- and 3-m

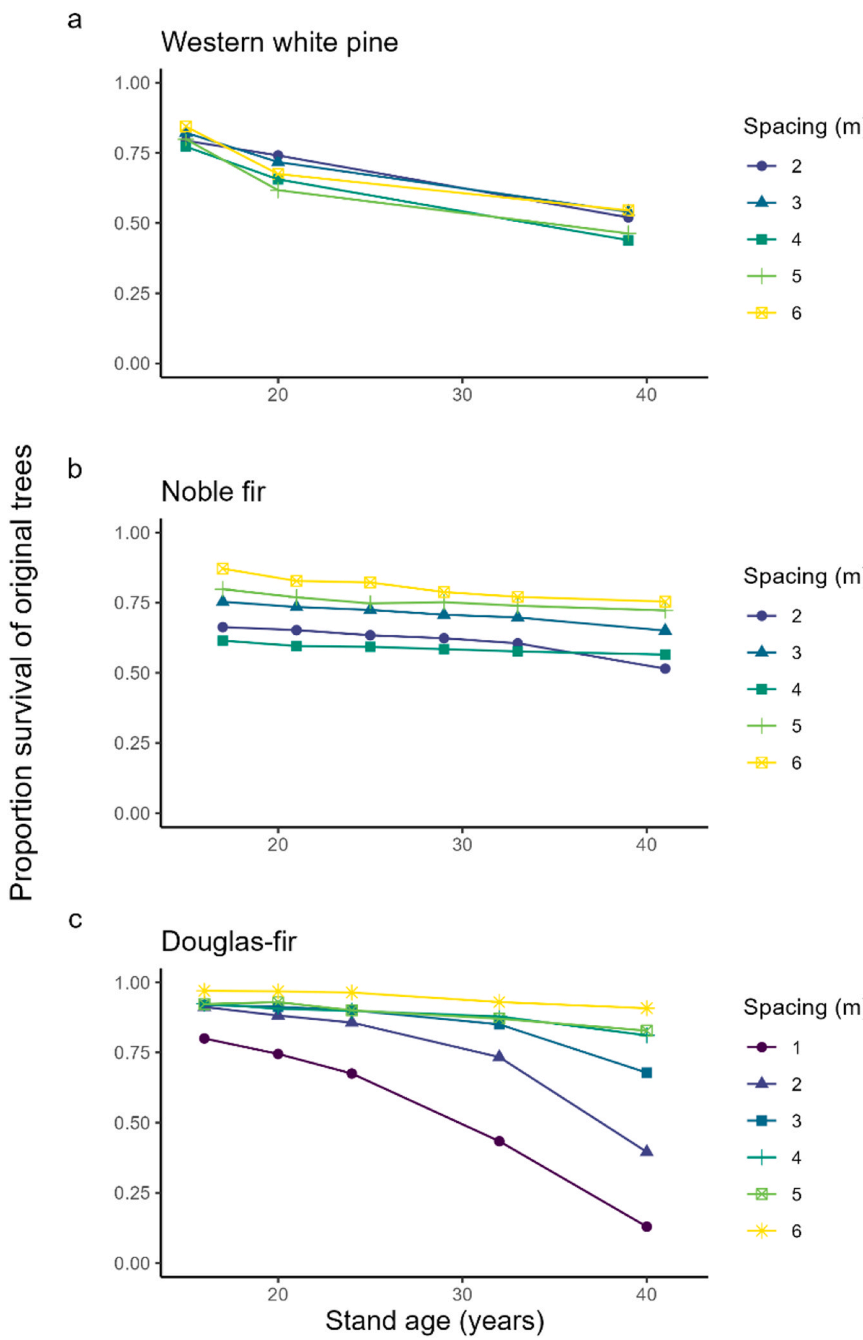

Fig. 1. Mean relative survival of originally planted seedlings for a) western white pine, b) noble fir, and c) Douglas-fir by spacing treatment and measurement year (stand age). There was a significant effect of spacing within a measurement period on Douglas-fir survival, but no effect on western white pine or noble fir survival. Significant differences among spacing treatments for each measurement period are shown in Supplemental Tables S3–5.

spacings than in the 5- and 6-m spacings. There was no effect of spacing treatment on HLC for NF.

Spacing treatment had a significant effect on total stand wood volume of trees > 4 cm DBH for all species that was dependent on measurement period. Volume generally decreased as spacing increased, with differences among treatments becoming larger with time (Fig. 4). However, there are many nuances to this general pattern. For WWP, total wood volume decreased with increased spacing with the exception of 5- and 6-m spacings which were similar to each other and lowest throughout the study period. For NF, patterns of volume response to spacing treatment were not consistent over the study period; the 2-m spacing had higher volume than the 4–6-m spacings at stand age 17 and 21, but differences in later years were not significant due to high variation among plots. For DF, the 1-and 2-m spacing treatments had significantly higher volume than the 3–6 m spacing treatments between years 16–24, but volumes were similar among treatments in the most recent measurement because of increased mortality in the 1- and 2-m spacing treatments (Fig. 1). The exception was the 6-m spacing treatment, which had significantly lower volume than the 2–4-m treatments in the most recent measurement (Fig. 4). Unsurprisingly, basal area responses to the treatments were very similar to those for volume (see Supplemental Tables S3–5 for basal area estimates by species and treatments).

Spacing treatment had a significant effect on SDI for each of the three species that varied with stand age ($p < 0.001$ for all species, Supplemental Table S2). These effects reflect differences in live tree density and

Table 1
Mean live tree density (surviving planted + ingrowth >4 cm DBH) by species and spacing treatment at the end of 2021. Means containing different letters within a species are significantly different as determined using Tukey's HSD test at an alpha of 0.05.

		Live tree density (number per ha, 95 % CI in parentheses)		
Spacing Treatment	Trees planted	Western white pine	Noble fir	Douglas-fir
1-m	10,000	NA	NA	1988 (1678, 2354) a
2-m	2500	1467 (1314, 1638) a	1609 (1408, 1839) a	1192 (1038, 1368) b
3-m	1111	727 (672, 786) b	1015 (888, 1161) b	826 (742, 920) c
4-m	625	383 (343, 428) c	682 (596, 779) c	543 (473, 623) d
5-m	400	283 (254, 317) d	625 (546, 714) c	419 (365, 481) d
6-m	278	288 (258, 322) d	574 (499, 653) c	313 (272, 360) e

QMD among spacing treatments across the three species. Across all species, SDI increased as spacing decreased and generally increased over time within each spacing (Fig. 5). One notable departure from this general pattern is trends in narrower spacing within DF, where SDI significantly decreased at 1–2 m spacings since the previous measurement period.

3.3. Vegetation cover and richness (Douglas-fir only)

There were significant effects of spacing treatment on cover of shrubs and trees (Table S6), but multiple comparisons failed to detect differences among treatments for tree cover. Shrub cover was generally higher at wider spacings, but only significantly different between the 1-m and 3–6 m spacings (Table 2). The dominant shrub species across all spacings were salal and Oregon grape, which are common associations in this vegetation zone. There was no effect of spacing on herbaceous cover or total species richness (Table S6). The most common herbaceous species across all spacings were vanilla leaf (*Achlys triphylla*), bracken fern (*Pteridium aquilinum*), western sword fern (*Polystichum munitum*) and bear-grass. Douglas-fir and western hemlock were the only regenerating tree species observed across all spacing treatments.

4. Discussion

Spacing between tree seedlings at time of planting influences availability of growth-limiting resources that controls establishment success, stand development, and long-term forest function. Managers may choose a wide range of spacings depending on their objectives and resource constraints, underlying a need to understand individual tree and stand response to spacing treatments. Our findings indicate that spacing has long-term (>40 year) effects on survival and growth where wider tree spacings are associated with increased survival, diameter growth, and live crown length, and decreased total stand density (including ingrowth) and volume. Our results align with other studies in this region (Reukema and Smith, 1987, Woodruff et al., 2002, Maguire and Mainwaring, 2021, Omari et al., 2021) but, importantly, cover a longer time period that is representative of rotation lengths on industrial forestlands in the region. These general trends were consistent across the three species assessed, although the magnitude and significance of the response varied. We explore some of these differences by species and the relevance of responses to differing management objectives below.

4.1. Western white pine survival and growth

Of the three species, western white pine had the lowest overall relative survival across all spacing treatments. This higher level of mortality is related to the occurrence of white pine blister rust which infects all five-needle pine species, including western white pine. We did not assess the prevalence of blister rust here, but an earlier report documented that most mortality up to age 16 was associated with the pathogen (Bishaw et al., 2003). Some of the recent mortality in the narrow spacing treatments was likely caused by inter-tree competition given the high SDI values at those spacings, but we attribute most mortality to blister rust in the wider spacings where density-dependent mortality is not likely at the stocking levels in those treatments. Earlier reports from studies in Idaho have shown that blister rust-resistant stock (which was used in this study) can have survival rates of 75–90 % on average in stands from ~10–25 years in age (Fins et al., 2001), similar to other reports showing survival of 65–90 % in stands 8–14 years in age (Snizeko et al., 2012). The lower survival observed here may be associated with the longer study duration compared to others, differences in disease pressure due to the site climate or race of *C. ribicola* (Geils et al., 2010), or other mortality agents such as insect or bear damage (Bishaw and Harrington 2003). Regardless, it appears that modifying the spacing of planted trees during reforestation is not effective to reduce blister rust mortality in WWP.

Blister rust has and will continue to hamper WWP reforestation, but ongoing breeding programs for the development of blister rust-resistant populations create opportunities to establish and maintain this iconic species in the western US (Snizeko et al., 2020). Further, WWP is projected to fare well in future climate over most of its range (Loehman et al., 2011), highlighting a need for the development of silvicultural systems that allow for inclusion of the species in adaptation strategies. Given the mortality pressure of blister rust and other agents (e.g., mountain pine beetle [*Dendroctonous ponderosae*]), silvicultural systems that promote a mixed species composition with a large component of WWP and non-host species may be a good option to maintain WWP under future conditions. Our wide spacing treatments developed relatively large trees (Fig. 2) that will dominate the canopy, while also allowing for establishment of other species and development of vertical stand structure (R. Slesak, pers. obs, Supplemental Figure S2). Ingrowth across the 4–6-m spacings averaged 115 TPH and was predominately Douglas-fir (97 %, with remaining 3 % as WWP). These stand characteristics offer multiple trajectories for further development in the future. Alternatively, if the desire is to establish an even-aged stand of WWP, planting blister rust-resistant stock at higher densities, (i.e., the 2- or 3-m treatments) followed by thinning treatments at 30–40 years to remove *C. ribicola*-infected trees could be a viable alternative.

4.2. Noble fir survival and growth

The general trends in survival and growth across spacing treatments were not as pronounced and often not significant for NF, likely because of the large quantity of ingrowth in NF plots (Table 1). Noble fir crowns are narrower than many conifer species, which may have facilitated the establishment of ingrowth by allowing more light in the understory. Ingrowth was largely comprised of DF and western hemlock (WH), which were the dominant species of the stand that existed prior to treatment initiation and common tree associations in the region. The site is also outside the core habitat range of NF, occurring at a lower elevation (~700 m) than what is typical for the species (>900 m, Franklin and Dyrness, 1973). These factors likely contributed to the large amount of ingrowth and its composition. Ingrowth was similar across the spacing treatments (averaging ~540 TPH over the study period), which is somewhat surprising given the large differences in initial stocking among spacing treatments and similar rates of survival of planted seedlings. Examination of the diameter distributions by spacing treatment indicates relatively continuous recruitment over the course of the study, with the exception of the widest spacings which exhibit a bimodal distribution indicative of a two-cohort stand (Supplemental Figure S2). In general, the large amount of ingrowth limits any

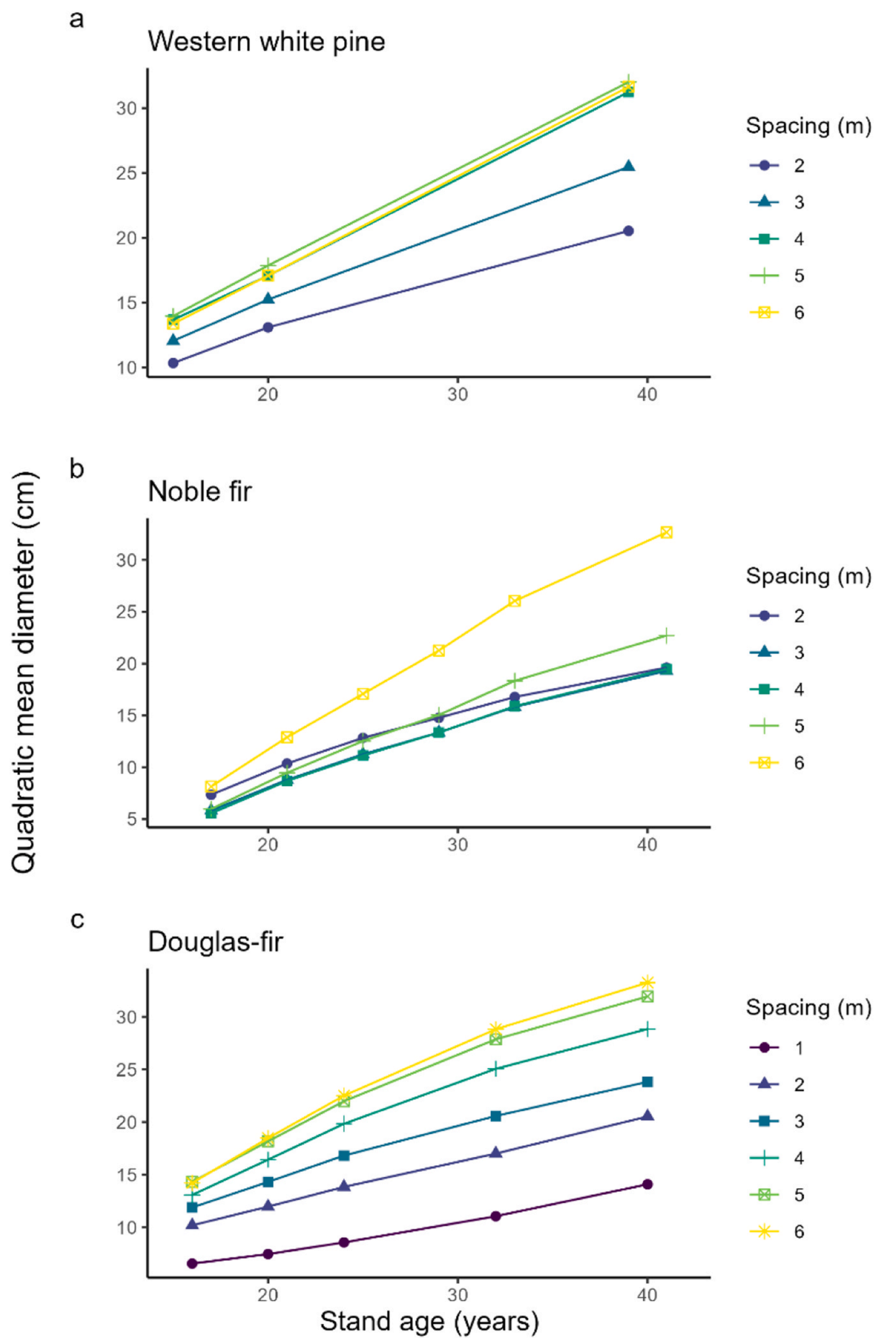

Fig. 2. Mean quadratic mean diameter (QMD) of planted trees for a) western white pine, b) noble fir, and c) Douglas-fir by spacing treatment and measurement period. There were significant effects of spacing on QMD in western white pine and Douglas-fir, but no detectable spacing effect in noble fir. Significant differences among spacing treatments for each measurement period are shown in Supplemental Tables S2–4.

conclusions on the effects of initial spacing on NF survival and growth.

Mortality of planted trees was fairly consistent across spacings, indicating that density has not reached a point where intraspecific competition has increased NF mortality. Stand density indices (e.g., Reineke's SDI; Reineke, 1933) that quantify the relationship between stand-level tree size (typically using QMD) and tree density can be used to predict the onset of density-dependent mortality (also referred to as self-thinning, typically occurring at 55–60 % of maximum SDI, Long 1985). Woodall and Weiskittel (2021) calculated max SDI for NF as 1300 TPH and 2047 TPH in the western Cascades and eastern Cascades, respectively. The 2-m spacing treatment in our study had an SDI of 1210 TPH (95 % CI: 734, 1994). Given this, and an assumed onset of density-dependent mortality at ~60 % SDI, our site aligns closer to max SDI reported for the eastern Cascades (Woodall and Weiskittel, 2021). Curtis (2013), reporting 20-yr response of NF to various spacing treatments (primarily created by thinning), concluded that NF in the Cascades is likely to have 20–25 % higher SDI maximums compared to DF (~1470 TPH, see below). Our results align with that conclusion, indicating that NF in this region has one of the highest max SDIs reported for forests in North America (Dean and Baldwin, 1996).

NF is projected to fare poorly under future climate (Kralicek et al., 2022, Crookston et al., 2010) because it is a subalpine species with limited ability for habitat expansion. However, the species is still dominant within its current habitat range and is planted for commercial production at higher elevation sites. Given that the study site is at lower elevation (higher temperature than typical) than its core habitat, and

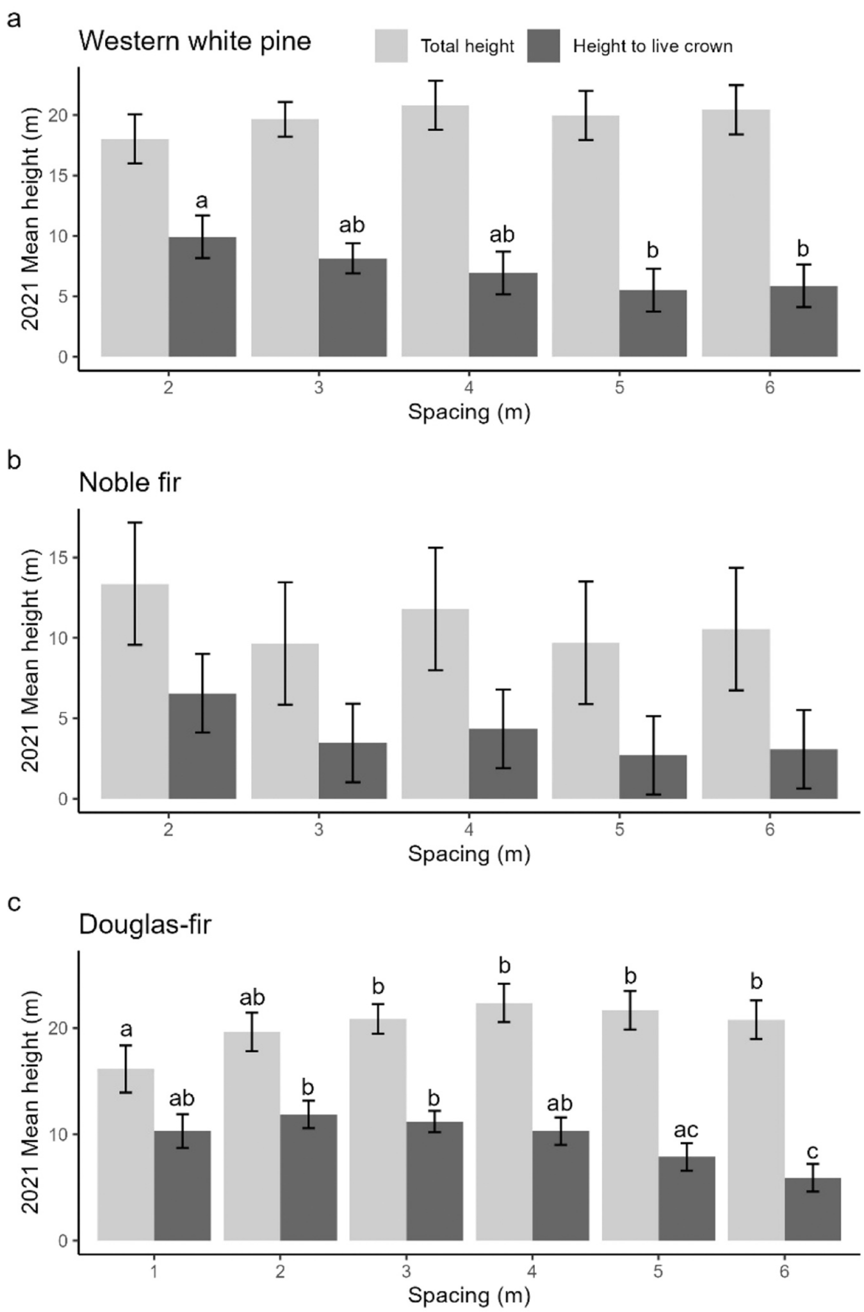

Fig. 3. Effects of spacing treatments on mean total height and height to live crown at the end of 2021 for a) western white pine, b) noble fir, and c) Douglas-fir. Heights estimated from a subset of originally planted trees only (see methods). Treatment means within a species that contain different letters are significantly different for the associated height variable. Means without letters indicate there was no main effect of treatment on that variable.

climate also warmed during the study period (increase of 0.7 C mean annual temperature and 1.1 C mean cold month temperature; comparison of 1961–1990 and 1991–2020 time periods; Mahony et al., 2022), the results reported here may reflect those expected under future conditions as NF habitat becomes more constrained to higher elevations.

4.3. Douglas-fir survival and growth

The effects of tree spacing on survival and growth in Douglas-fir align with earlier reports from the study (Harrington et al., 2009, Curtis et al., 2016) and anticipated changes in those effects with time. Harrington et al. (2009) observed density-dependent mortality in the 1-m spacing at year 25 when relative stand density index (Reineke, SDI) exceeded 52 % of the maximum for Douglas-fir (1470 TPH with QMD of 25 cm; Dean and Baldwin, 1996) and predicted similar future responses in the 2-m treatment. The observed exponential decrease in survival in the 2-m spacing treatment confirms this prediction; mortality in this treatment is likely to continue as relative SDI was 56 % during the most recent measurement. Note that some of the mortality in narrow spacings (1–2 m) was associated with higher incidence of snow and ice damage (M. Powers and R. Slesak, pers. obs.), which is an indirect outcome of intraspecific competition that has been reported previously (Miller et al., 2004) arising from increased height:diameter ratios (Priebe et al., 2018). The lower relative survival in the 3-m treatment relative to the 6-m treatment is likely also associated with density-dependent mortality as the 3-m treatment currently has a relative max SDI of ~50 %. In contrast, max SDI in the 4–6 m spacings (SDI% of 44, 37, and 29 for the 4-, 5-, and 6-m spacings, respectively) indicate that mortality arising

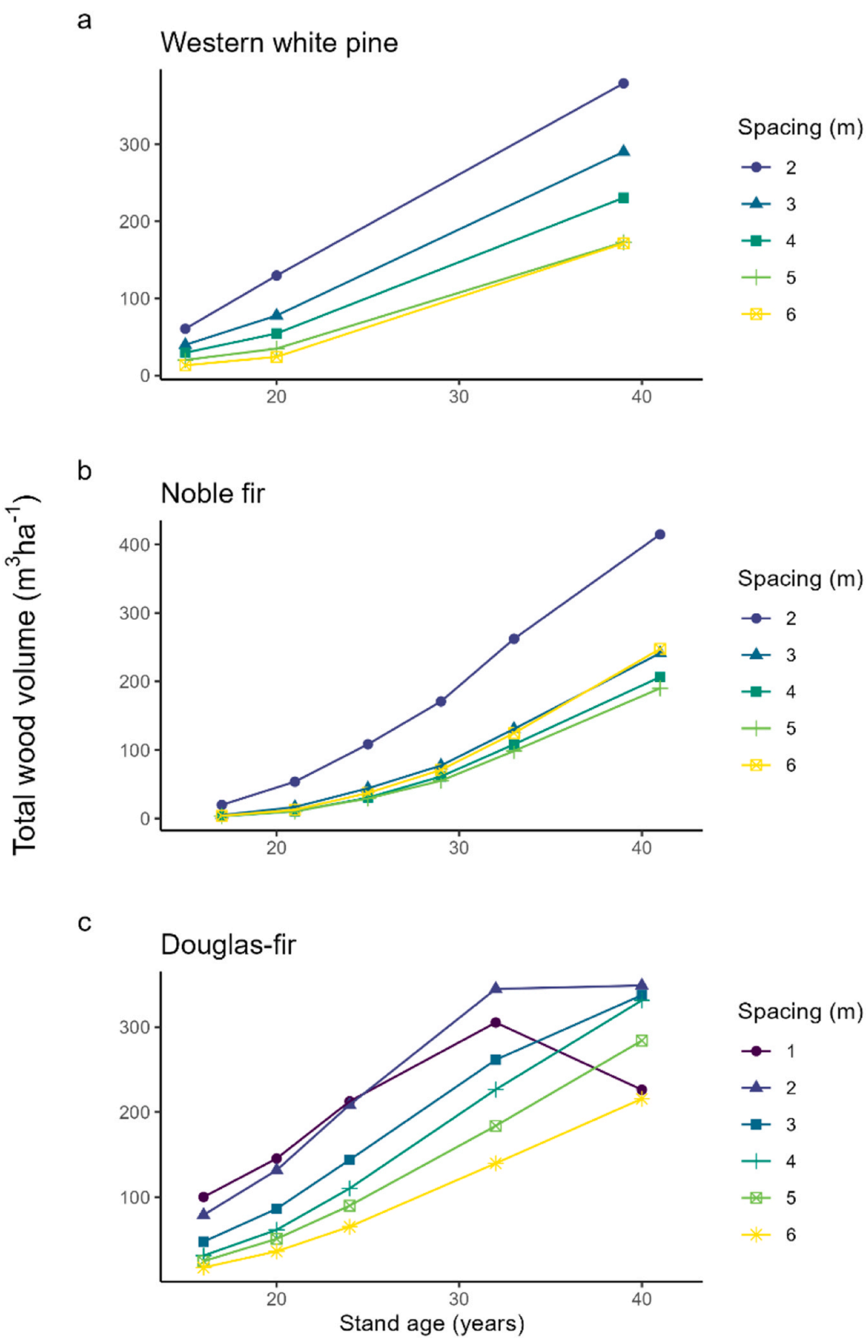

Fig. 4. Mean total stand wood volume of planted trees and ingrowth for a) western white pine, b) noble fir, and c) Douglas-fir by spacing treatment and measurement period. There were significant effects of spacing on volume in western white pine and Douglas-fir, but no spacing effect in noble fir. Significant differences among spacing treatments for each measurement period are shown in Supplemental Tables S3–5.

from inter-tree competition will remain low for some time into the future.

Higher individual tree growth (as evidenced by mean QMD) in the wider (4–6 m) spacing treatments arose from greater resource availability to a smaller number of trees in those treatments relative to narrower (1–3 m) spacing treatments. Similar findings were previously reported in this study (Harrington et al., 2009, Curtis et al., 2016) and also observed in other spacing studies (Reukema and Smith, 1987, Scott et al., 1998, Woodruff et al., 2002). However, earlier reports (this study and others) found an opposite trend in total stand volume where narrower spacings (1–3 m) had the highest volumes due to limited difference in height among treatments coupled with higher total stand densities at narrow spacings. Apparently in this most recent measurement, increased mortality in narrow spacings coupled with increased growth in wider spacings has evened out differences in total volume among treatments (Fig. 4), with the exception of lower volume in the 6-m spacing compared to other spacings (Table S3). Further, Curtis et al. (2016) showed that *merchantable* volume (trees >20 cm DBH) was greatest in the 4-m spacing treatment at year 33; this effect has continued in the most recent measurement where the 4-m spacing merchantable volume was ~7 % greater than the 3-m spacing (data not shown). Larger trees in the wider spacing treatments may provide greater economic benefit and longer live crowns that may impart improved resistance to extreme events. Increased diameters in wider spacings also contribute to lower height to diameter ratios increasing windfirmness (Harrington et al., 2009) and reducing the risk of damage

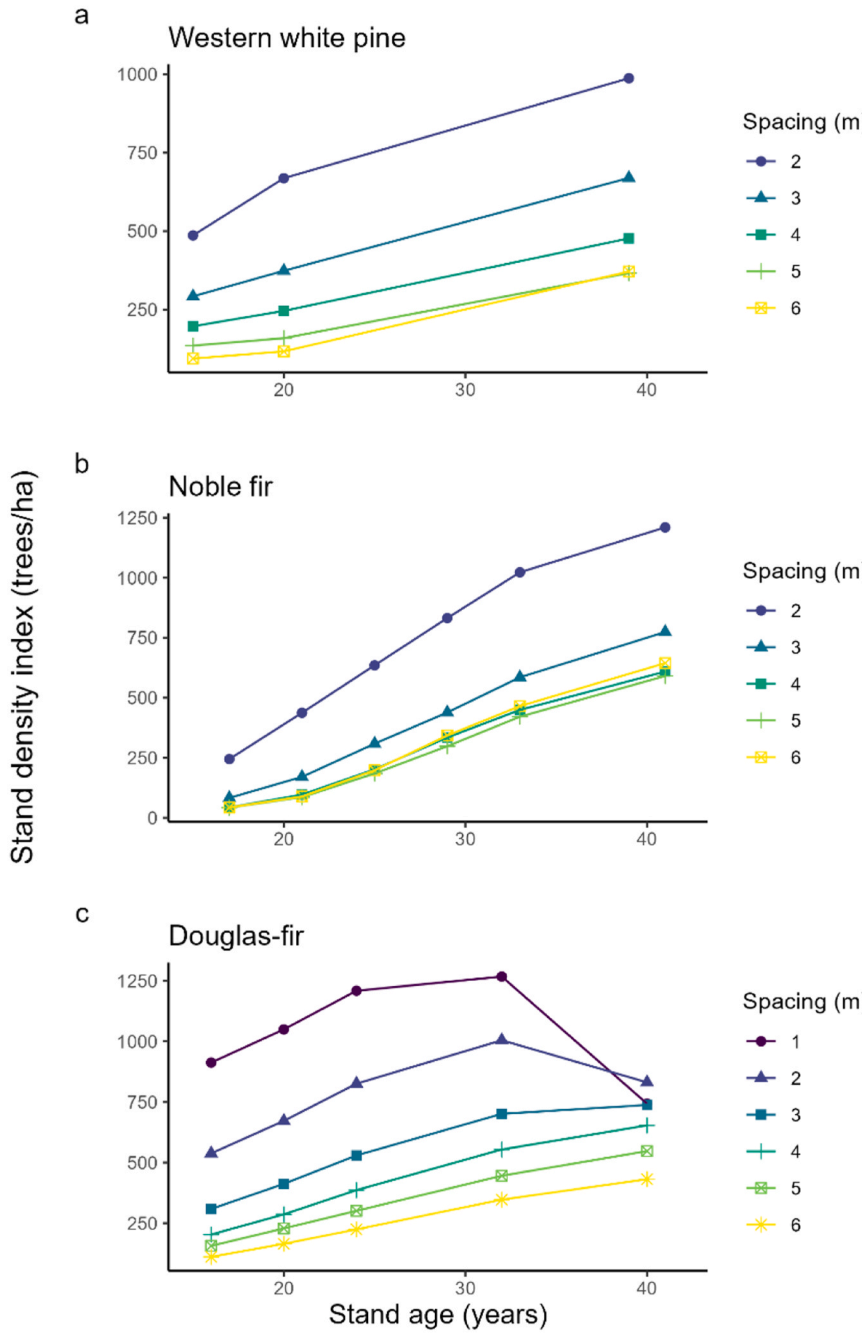

Fig. 5. Stand Density Index (SDI) by spacing treatment and stand age for a) western white pine, b) noble fir, and c) Douglas-fir. There were significant effects of spacing on SDI for each species and stand age.

during glaze events (Priebe et al., 2018).

The limited effects of spacing treatment on understory cover and diversity were surprising, as we expected greater light availability in the wider spacings to promote those features. We are unaware of other spacing studies that have evaluated understory response to planting density. Thinning studies that reduce stand density and crown cover have shown mixed results on understory response, likely dependent on the magnitude and duration of crown reduction and concurrent changes in the understory environment as the overstory eventually returns to closed canopy (Lindh and Muir, 2004, Bailey et al., 1998). Given this, the limited effects observed here are likely due to similar overstory cover across spacings in the most recent measurement (~80 % canopy cover across 2–5 m spacings, Table 2), which would mediate understory light conditions across treatments. Despite this, it appears that the wider spacings are likely to more rapidly develop vertical structure compared to the narrow spacings; diameter distributions indicate recruitment of a smaller (younger) cohort in the 5–6 m spacings (Supplemental Figure S2) which is largely composed of western hemlock and DF with minor components of Pacific silver fir, western white pine, and western red cedar (data not shown). As with larger tree size at wider spacings, this structural development may provide more favorable habitat for various wildlife species (Culbert et al., 2013, Hagar, 2007), or improved resistance to wildfire (Dunn and Bailey 2016).

4.4. *Management implications*

Ultimately management objectives combined with resource constraints will dictate what tree spacing (planting density) is used during

Table 2
Mean vegetation cover and species richness by spacing treatment at the end of 2021. Means containing different letters are significantly different as determined using Tukey's HSD test at an alpha of 0.05; means without letters indicate no significant effect of spacing treatment on the associated variable.

Spacing treatment	Proportion herb cover	Proportion shrub cover	Proportion tree cover	Total species richness (#)
1-m	0.29 (0.16–0.47)	0.50 (0.32–0.68) a	0.62 (0.40–0.80)	10.8 (8.7–12.8)
2-m	0.21 (0.11–0.34)	0.76 (0.61–0.86) ab	0.80 (0.64–0.90)	10.8 (9.1–12.5)
3-m	0.31 (0.19–0.46)	0.88 (0.77–0.94) b	0.81 (0.66–0.91)	9.5 (7.8–9.2)
4-m	0.20 (0.11–0.30)	0.91 (0.82–0.96) b	0.83 (0.68–0.92)	10.2 (8.5–11.9)
5-m	0.30 (0.18–0.44)	0.83 (0.70–0.91) b	0.81 (0.65–0.90)	9.7 (8.0–11.4)
6-m	0.33 (0.21–0.48)	0.88 (0.78–0.94) b	0.51 (0.33–0.68)	10.5 (8.8–12.2)

reforestation. When objectives are to maximize economic benefit (maximum fiber production or return on investment), a spacing that maximizes growth while reducing the need for intermediate (to final harvest) treatments would be favorable. In that case, the 4-m spacing treatment may be ideal, as it is associated with high volume growth (similar to the 3-m spacing which is more typical) while avoiding density-dependent mortality observed in 1–3-m spacings during the first ~40 years of stand development and which is expected to continue into the future. This assumes neutral to beneficial effects of wider spacings on wood morphological characteristics that influence value, which has been shown in some studies (Isaac-Renton et al., 2020) but will vary depending on the products being developed (e.g., pulp vs. structural lumber vs. bioenergy). However, the more typically used 3-m spacing may have greater utility if thinning is planned and /or practical, or if managers wish to retain a larger number of trees that allow for more silvicultural options over the course of a rotation.

Most public forest management agencies have broad objectives focused on maintenance of functional forest ecosystems, and at the same time face resource constraints to achieve their objectives. This combination of factors favors planting at wider spacings to avoid a possible need for intermediate treatments such as thinning. Based on our results, planting at wider spacings will promote the more rapid development of larger trees and more complex forest structure, which provides additional benefits including wildlife habitat and increased resistance to extreme weather events (wind, drought, and winter storms). Given this, wider tree spacings (5- to 6-m) may be ideal to achieve this objective with limited resources. There is one important caveat with this statement: survival needs to be relatively high to achieve these benefits. For this study, both chemical and mechanical vegetation control were periodically applied in the first decade to limit early mortality associated with competition. A large number of studies in the PNW region have shown that vegetation control immediately before or after planting is essential for successful establishment (Harrington and Schoenholtz 2010, Maguire et al., 2009, Yildiz et al., 2011). Control is likely to be even more important when planting at low densities, as there are more resources and space for competing vegetation to develop. To be successful, managers planting at wide spacings should carefully evaluate the competitive environment at the associated site and plan for pre- or post-establishment control of competing vegetation.

The role of site quality cannot be quantified here given that the study only occurred on one site of moderate productivity (Curtis et al., 2016), but it is an important consideration as noted in other spacing studies (Reukema and Smith, 1987, Harrington et al., 2009). Sites of higher quality (reflecting greater resource availability) generally accelerate the effects of spacing on mortality and tree size (Harrington et al., 2009), suggesting that lower quality sites may be more appropriate for wider spacings in the absence of vegetation control or planned intermediate treatments. At higher quality sites, the necessity of these practices will be dependent on the spacing choice, with wider spacings requiring high levels of vegetation control and narrower spacings requiring thinning.

5. Conclusion

This study quantified spacing effects over four decades after planting for three important conifer species in the Pacific Northwest, providing information that is directly relevant to management time scales (i.e., rotation length responses). The long duration of these trials has proved invaluable in clarifying decadal responses, and continued measurement will provide a rare opportunity to quantify the long-term effects of initial spacing on stand dynamics. Spacing at time of planting has large and long-term effects on individual and stand level growth for each of the species in this study. Increased spacing increases individual tree survival, diameter, and live crown length, and decreases overall stand volume. In the case of volume for DF, this general pattern is changing as density-dependent mortality has increased in narrower spacings to the extent that total volume is now similar across treatments (i.e., the crossover effect). We expect that these findings will help to inform choice of spacing during reforestation across a wide range of management objectives, resource constraints, and site conditions.

CRediT authorship contribution statement

Agne Michelle C.: Writing – review & editing, Visualization, Methodology, Formal analysis. **Slesak Robert A.:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition. **Powers Matthew D.:** Writing – review & editing, Resources, Investigation. **Harrington Constance A.:** Writing – review & editing, Methodology, Investigation, Conceptualization.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122724.

Data availability

Data will be made available on request.

References

Bailey, J.D., Mayrsohn, C., Doescher, P.S., Pierre, E.S., Tappeiner, J.C., 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. For. Ecol. Manag. 112 (3), 289–302. https://doi.org/10.1016/S0378-1127(98)00408-3.

Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., Zedaker, S.M., 2006. Designing forest vegetation management strategies based on the mechanisms and dynamics of

crop tree competition by neighbouring vegetation. For.: Int. J. For. Res. 79 (1), 3–27. https://doi.org/10.1093/forestry/cpi056.
Bishaw, B., DeBell, D.S., Harrington, C.A., 2003. Patterns of survival, damage, and growth for western white pine in a 16-year old spacing trial in western Washington. West. J. Appl. For. 18 (1), 35–43.
Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9, 378–400.
Browne, J.E., 1962. Standard cubic-foot volume tables for the commercial species of British Columbia, 1962. British Columbia Forest Service, Victoria, BC, p. 107.
Bruce, D., DeMars, D.J., 1974. Volume equations for second-growth Douglas-fir. Pacific Northwest Forest and Range Experiment Station, Forest Service. US Department of Agriculture, p. 5. Research Note PNW-239.
Crookston, N.L., Rehfeldt, G.E., Dixon, G.E., Weiskittel, A.R., 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. For. Ecol. Manag. 260, 1198–1211. https://doi.org/10.1016/j.foreco.2010.07.013.
Culbert, Patrick, D., Radeloff, Volker, C., Flather, Curtis, H., Kellndorfer, Josef, M., Rittenhouse, Chadwick, D., Pidgeon, Anna M., 2013. The influence of vertical and horizontal habitat structure on nationwide patterns of avian biodiversity. The Auk 130 (4), 656–665.
Curtis, R.O., 2006. Volume growth trends in a Douglas-fir levels-of-growing-stock study. West. J. Appl. For. 21 (2), 79–86.
Curtis, Robert O. 2013. True fir spacing and yield trials—20-year update. Res. Pap. PNW-RP-590. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 32 p.
Curtis, Robert, O., Sheel, Bansal, Harrington, Constance, A., 2016. Relation of initial spacing and relative stand density indices to stand characteristics in a Douglas-fir plantation spacing trial. Res. Pap. PNW-RP-607. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, p. 27.
D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecol. Appl. 23 (8), 1735–1742.
Dean, T.J., Baldwin Jr., V.C., 1996. The relationship between Reineke's stand-density index and physical stem mechanics. For. Ecol. Manag. 81, 25–34.
Dobrowski, S.Z., Aghai, M.M., Chichilnisky du Lac, A., Downer, R., Fargione, J., Haase, D.L., Hoecker, T., Kildisheva, O.A., Murdoch, A., Newman, S., North, M., 2024. Mind the gap'—reforestation needs vs. reforestation capacity in the western United States. Front. For. Glob. Change 7, 1402124.
Dodson, E.K., Ares, A., Puettmann, K.J., 2012. Early responses to thinning treatments designed to accelerate late successional forest structure in young coniferous stands of western Oregon, USA. Can. J. For. Res. 42 (2), 345–355. https://doi.org/10.1139/x11-188.
Erickson, H.E., Harrington, C.A., 2006. Conifer-*Ceanothus* interactions influence tree growth before and after shrub removal in a forest plantation in the western Cascade Mountains. USA. For. Ecol. Mngt. 229, 183–194. https://doi.org/10.1016/j.foreco.2006.03.029.
Fargione, J., Haase, D.L., Burney, O.T., Kildisheva, O.A., Edge, G., Cook-Patton, S.C., Chapman, T., Rempel, A., Hurteau, M.D., Davis, K.T., Dobrowski, S., Enebak, S., De La Torre, R., Bhuta, A.A.R., Cubbage, F., Kittler, B., Zhang, D., Guldin, R.W., 2021. Challenges to the reforestation pipeline in the United States. Front. For. Glob. Change 4, 629198.
Fins, L., J. Byler, D. Ferguson, A. Harvey, M.F. Mahalovich, G. Mcdonald, D. Miller, J. Schwandt, and A. Zack. 2001. Return of the giants - restoring white pine ecosystems by breeding and aggressive planting of blister rust-resistant white pines. Sta. Bull. 72, Idaho For.,Wildlife, and Range Exp. Sta., Univ. of Idaho, Moscow. 20 p.
Franklin, J.F., Dyrness, C.T., 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, p. 417.
Gabira, M.M., Girona, M.M., DesRochers, A., Kratz, D., da Silva, R.B.G., Duarte, M.M., de Aguiar, N.S., Wendling, I., 2023. The impact of planting density on forest monospecific plantations: an overview. For. Ecol. Manag. 534, 120882. https://doi.org/10.1016/j.foreco.2023.120882.
Geils, B.W., Hummer, K.E., Hunt, R.S., 2010. White pines, Ribes, and blister rust: a review and synthesis. For. Pathol. 40, 147–185. https://doi.org/10.1111/j.1439-0329.2010.00654.x.
Hagar, J.C., 2007. Key Elements of Stand Structure for Wildlife in Production Forests West of the Cascade Mountains. In: Harrington, T.B., Nicholas, G.E. (Eds.), General Technical Report PNW-GTR-695. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA, pp. 35–48.
Harrington, T.B., Harrington, C.A., DeBell, D.S., 2009. Effects of planting spacing and site quality on 25-year growth and mortality relationships of Douglas-fir (Pseudotsuga menziesii var. Menziesii). For. Ecol. Manag. 258, 18–25. https://doi.org/10.1016/j.foreco.2009.03.039.
Isaac-Renton, M., Stoehr, M., Statland, C.B., Woods, J., 2020. Tree breeding and silviculture: Douglas-fir volume gains with minimal wood quality loss under variable planting densities. For. Ecol. Manag. 465, 118094.
Kralicek, Karin, Barrett, Tara M., Ver Hoef, Jay M., Temesgen, Hailemariam, 2022. Forests at the fringe: Comparing observed change to projected climate change impacts for five tree species in the Pacific Northwest, United States. Front. For. Glob. Change 5, 966953.
Lindh, B.C., Muir, P.S., 2004. Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? For. Ecol. Manag. 192, 285–296. https://doi.org/10.1016/j.foreco.2004.01.018.
Loehman, R.A., Clark, J.A., Keane, R.E., 2011. Modeling effects of climate change and fire management on western white pine (Pinus monticola) in the northern Rocky Mountains, USA. Forests 2, 832–860.
Maguire, D.A., Mainwaring, D.B., Rose, R., Garber, S.M., Dinger, E.J., 2009. Response of coastal Douglas-fir and competing vegetation to repeated and delayed weed control treatments during early plantation development. Can. J. For. Res. 39 (6), 1208–1219.
Maguire, D.A., Mainwaring, D.B., 2021. Effects of initial spacing and species mix on stand developmental patterns in two field trials in central Oregon. For. Ecol. Manag. 491, 119153. https://doi.org/10.1016/j.foreco.2021.119153.
Mahony, C.R., Wang, T., Hamann, A., Cannon, A.J., 2022. A CMIP6 ensemble for downscaled monthly climate normals over North America. Int. J. Climatol. 42 (11), 5871–5891. https://doi.org/10.1002/joc.7566.
Miller, R.E., Reukema, D.L., Anderson, H.W., 2004. Tree growth and soil relations at the 1925 Wind River spacing test in coast Douglas-fir. Res. Pap. PNW-RP-558. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, p. 41.
North, M.P., Stevens, J.T., Greene, D.F., Coppoletta, M., Knapp, E.E., Latimer, A.M., Restaino, C.M., Tompkins, R.E., Welch, K.R., York, R.A., Young, D.J.N., Axelson, J. N., Buckley, T.N., Estes, B.L., Hager, R.N., Long, J.W., Meyer, M.D., Ostoja, S.M., Safford, H.D., Shive, K.L., Tubbesing, C.L., Vice, H., Walsh, D., Werner, C.M., Wyrsch, P., 2019. Tamm Review: Reforestation for resilience in dry western U.S. forests. For. Ecol. Manag. 432, 209–224. https://doi.org/10.1016/j.foreco.2018.09.007.
North, M.P., Tompkins, R.E., Bernal, A.A., Collins, B.M., Stephens, S.L., York, R.A., 2022. Operational resilience in Western US frequent-fire forests. For. Ecol. Manag 507, 120004. https://doi.org/10.1016/j.foreco.2021.120004.
Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. John Wiley and Sons, Inc, New York.
Omari, K., Kranabetter, J.M., de Montigny, L., 2021. Productivity of coastal Douglas-fir and western redcedar in response to species mixture, planting density, and soil carbon:nitrogen ratio. Can. J. For. Res. 51 (5), 668–674. https://doi.org/10.1139/cjfr-2020-0223.
Priebe, J.E., Powers, M.D., Cole, E.C., 2018. Species, tree size, and overstory environment affect likelihood of ice storm damage to understory trees in a mature Douglas-fir forest. For. Ecol. Manag. 409, 777–788. https://doi.org/10.1016/j.foreco.2017.11.041.
Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.
Reukema, D.L. 1979. Fifty-year development of Douglas-fir stands planted at various spacings. USDA For. Serv. Res. Pap. PNW-253, 21 p., Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
Reukema, D.L., and Smith, J.H.G. 1987. Development over 25 years of Douglas-fir, western hemlock, and western redcedar planted at various spacings on a very good site in British Columbia. Res, Pap. PNW-RP-381, Pacific Northwest Research Station, USDA, Portland, Ore.
Rubilar, R.A., Allen, H.L., Fox, T.R., Cook, R.L., Albaugh, T.J., Campoe, O.C., 2018. Advances in silviculture of intensively managed plantations. Curr. For. Rep. 4, 23–34. https://doi.org/10.1007/s40725-018-0072-9.
Scott, W., Meade, R., Leon, R., Hyink, D., Miller, R., 1998. Planting density and tree-size relations in coast Douglas-fir. Can. J. For. Res. 28, 74–78.
Sniezko, R.A., Danchok, R., Hamlin, J., Kegley, A., Long, S., Mayo, J., 2012. White pine blister rust resistance of 12 western white pine families at three field sites in the Pacific Northwest. Gen. Tech. Rep. PSW-GTR 240.
Sniezko, R.A., Johnson, J.S., Savin, D.P., 2020. Assessing the durability, stability, and usability of genetic resistance to a non-native fungal pathogen in two pine species. Plants, People, Planet 2, 57–68. https://doi.org/10.1002/ppp3.49.
Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Official Soil Series Descriptions – Stabler Series. Available online at ⟨https://soilseries.sc.egov.usda.gov/OSD_Docs/S/STABLER.html⟩. Accessed May 24,2024.
Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2001. Stand structure and small mammals in young lodgepole pine forest: 10-year results after thinning. Ecol. Appl. 11, 1151–1173. https://doi.org/10.1890/1051-0761(2001)011[1151:SSASMI]2.0.CO;2.
USDA Forest Service, 2022. National Forest System Reforestation Strategy Growing and nurturing resilient forests. USDA Forest Service National Forest System, Washington, DC. FS-1198, 32.
Wagner, R.G., Mohammed, G.H., Noland, T.L., 1999. Critical period of interspecific competition for northern conifers associated with herbaceous vegetation. Can. J. For. Res. 29, 890–897. https://doi.org/10.1139/x99-055.
Woodall, C.W., Weiskittel, A.R., 2021. Relative density of United States forests has shifted to higher levels over last two decades with important implications for future dynamics. Sci. Rep. 11 (1), 1444. https://doi.org/10.1038/s41598-021-98244-w.
Woodruff, D.R., Bond, B.J., Ritchie, G.A., Scott, W., 2002. Effects of stand density on the growth of young Douglas-fir trees. Can. J. For. Res. 32, 420–427.
Wykoff, W.R., N.L. Crookston, and A.R. Stage. 1982. User's guide to the stand prognosis model. USDA For. Serv. Gen. Tech. Rep. INT-133. 89 p.
Yildiz, O., Cromack Jr, K., Radosevich, S.R., Martinez-Ghersa, M.A., Baham, J.E., 2011. Comparison of 5th-and 14th-year Douglas-fir and understory vegetation responses to selective vegetation removal. For. Ecol. Manag. 262 (4), 586–597.