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Douglas-fir dominates when grown in dual species mixtures with three western conifers

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ABSTRACT

Planting a mixture of species during reforestation is of increasing interest, underlying a need to quantify the long-term effects of mixtures on stand development for a wide array of species. Here we report on ~40 year response of three dual species mixture trials at a moderate quality site in Washington, USA where coast Douglas-fir (DF, *Pseudotsuga menziesii* var. *menziesii*) was grown at 3 m spacing in a 50:50 mix with either western hemlock (WH, *Tsuga heterophylla*), noble fir (NF, *Abies procera*) or western white pine (WWP, *Pinus monticola*). Stand metrics were compared for each trial between replicated plots of the mixture and pure monocultures of each component species. Across all trials, DF grown in a mixture had greater height and diameter growth than any of the companion species (in either mixture or monocultures) and also outperformed DF grown in a monoculture. Height to diameter ratios for DF were lower in mixtures for all trials compared to DF monocultures, indicating lower interspecific competition for light when grown in mixture. In the DF-NF and DF-WWP trials, mixtures had lower total volume than the DF monoculture, but higher total volume than the NF and WWP monocultures. In contrast, there were no differences in volume between the mixture and monocultures in the DF-WH trial, likely because of complementary shade tolerances between species; overyielding in the mixture may occur with further stand development. These findings can inform decisions on the utility of species mixtures to achieve various management objectives related to wood production.

1. Introduction

The decision on what to plant when reforesting is a central aspect of forestry. Forest managers typically plant a single species with the intent to develop a monoculture stand given the ease and efficiency with which they are managed (Kelty, 2006). Because of this, much past silvicultural research has focused on developing and measuring monospecific stands, with limited studies focused on planted, mixed-species stands. Management of species mixtures (two or more planted tree species) is of increasing interest given perceived benefits such as greater resilience to stressors (e.g., pests, changing climate), greater biodiversity, and reduced market risk, among others (Carnol et al., 2014; Liu et al., 2018). Recognition of these benefits has led to widespread establishment of mixed-species forests in Europe and calls for broader implementation globally (Messier et al., 2022).

There is a need to quantify the effects of mixed-species plantings on stand development and productivity over a range of conditions so managers can make informed decisions on their utility. Rotation-length responses are critical to assess as competitive interactions between species will likely change as stands develop over time (Cavard et al., 2011; Forrester, 2014). Stand-level responses are dependent on the traits of each component species and the degree to which they complement or compete with each other (Cavard et al., 2011). The degree to which species differentiate in their characteristics is a central concept underlying the use of mixtures, potentially allowing for greater utilization of growth-limiting site resources (Kelty, 2006). For example, shade-tolerant and shade-intolerant species may complement each other in a mixture as overall light interception (arising from a stratified canopy) is increased relative to monoculture stands (Pretzsch, 2014; Williams et al., 2021). The potential for complementary effects (also referred to as overyielding), where a mixture of species has higher stand-level productivity relative to monocultures of each component species, can also depend on the density and ratio of the component species (Amoroso and Turnblom, 2006; Barbeito et al., 2021; Maguire and Mainwaring, 2021), stand age (Feng et al., 2022), and characteristics or properties that influence site quality (Jactel et al., 2018). Using

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meta-analysis, Feng et al. (2022) found that mixtures performed better on average than monocultures, with the greatest effect in mixtures with contrasting leaf characteristics between species (e.g., broadleaved vs. needle bearing, evergreen vs. deciduous). Other meta-analyses have also concluded that mixtures often result in beneficial effects to stand productivity (Piotto, 2008; Jactel et al., 2018).

In the Pacific Northwest (PNW), USA, coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) is the most commonly managed species in production-oriented forestry west of the Cascade Mountains. The species is classed as intermediate in shade tolerance but grows best under full sunlight and has rapid juvenile growth (Minore, 1979). Regeneration is generally conducted via planting following clearcutting after rotation lengths of 40 – 60 years. Douglas-fir occurs naturally in a large number of plant associations including western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), western white pine (*Pinus monticola*), and true firs (*Abies* spp.) (see Franklin and Dyrness, 1973 for detailed type classifications). Given the above, Douglas-fir grown in a mixture may be an option to increase biodiversity while maintaining or increasing overall stand productivity, but the viability of such an option is unclear. Himes and Puettmann (2020) found similar aboveground biomass among monocultures and mixtures of Douglas-fir, western hemlock and red alder (*Alnus rubra*) at ages 35 – 39. Amoroso and Turnblom (2006) also observed no difference in stand metrics when comparing monocultures and mixtures of Douglas-fir and western hemlock at age 12, but only at high planting densities. At lower densities more typical of operational practice, mixed stands had reductions in stand productivity compared to the Douglas-fir monoculture (Amoroso and Turnblom, 2006). Similarly, Omari et al. (2021), assessing Douglas-fir – western redcedar mixtures at age 22, observed significantly lower stand productivity in the mixture relative to the Douglas-fir monoculture. Given the range of responses identified in past work, more studies are needed to evaluate stand dynamics when growing Douglas-fir in a mixture in the Pacific Northwest region.

A series of dual-species mixture trials were established in 1980 – 1982 at a moderately productive site in the western Cascade Mountains of Washington, USA. The trials established 50:50 mixtures of Douglas-fir (DF) grown with either western hemlock, western white pine, or noble fir (*Abies procera*) along with pure stands of each of the component species for comparison. Erickson et al. (2009) previously reported the 20-year response of the western white pine (WWP) mixture and the 24-year response of the western hemlock (WH) mixture. They found no differences between the WWP-DF mixture and monocultures of each component species, but significantly greater growth for the WH-DF mixture versus the WH monoculture for most stand-level variables (e.g., mean diameter, mean height, total volume) (Erickson et al., 2009). The lack of difference between the WH-DF mixture and DF monoculture was attributed to greater growth of DF in the mixture, which offset lower growth of WH (Erickson et al., 2009).

Here we report on longer-term (> 40 years) responses of these trials and expand to include the noble fir (NF) mixture trial, which has not been previously reported. Our objective was to evaluate growth responses of Douglas-fir grown in mixed-species stands relative to pure stands of each component species over an approximate rotation length time period to provide information directly relevant to operational practice. We expected that there would be differences in growth response among the mixtures associated with differences in their functional traits (e.g. shade tolerance), and that there would be differences in growth response compared with earlier trends, as competitive interactions within the mixtures typically become more pronounced with time (Forrester, 2014).

2. Methods

2.1. Study site description

The trials are located in the Wind River Experimental Forest, Washington USA (45.828 °N, −121.997 °E), north of the Columbia River. 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 from May – September); annual precipitation is 2510 mm with 270 mm falling from May – September (monthly normals 1991–2020, PRISM 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 ranges 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, western hemlock, and Pacific silver fir (*Abies amabilis*), with minor components of western redcedar, noble fir and grand fir (*Abies grandis*). Large western white pine snags killed by white pine blister rust were present in the overstory, but no large living trees remained (Bishaw et al., 2003; Erickson et al., 2009). Other woody species included Pacific yew (*Taxus brevifolia*), vine maple (*Acer circinatum*), Pacific dogwood (*Cornus nuttallii*), salal (*Gaultheria shallon*), Oregon grape (*Mahonia aquifolium*), red huckleberry (*Vaccinium parvifolium*), big huckleberry (*Vaccinium membranaceum*) and Pacific rhododendron (*Rhododendron macrophyllum*) as shrubs or small trees and vanilla leaf (*Achlys triphylla*), Queens cup bead lily (*Clintonia uniflora*), sword fern (*Polystichum munitum*), bracken fern (*Pteridium aquilinum*), twinflower (*Linnea borealis*), western prince's pine (*Chimaphila umbellata*), and beargrass (*Xerophyllum tenax*) as understory species (Shaw et al., 2004). The site is of moderate productivity, site class 3 (King, 1966). The units were clearcut in 1978 or 1979, burned in 1979 or 1980, and planted in 1980, 1981 or 1982 depending on species (see details below).

2.2. Species characteristics

Species characteristics are critical aspects influencing stand productivity of mixtures (Kelty, 2006); we include the following brief descriptions of each conifer species for context and interpretation. Coast Douglas-fir is dominant west of the Cascade Mountains in the PNW region where it is commercially grown on rotations of 40 – 60 years. The species has rapid juvenile growth when grown in full sunlight and has intermediate shade tolerance (Franklin and Dyrness, 1973). Douglas-fir can naturally form pure stands, but depending on the climatic zone is often found with co-occurring species including western hemlock, western white pine, noble fir, western redcedar, and ponderosa pine (*Pinus ponderosa*). Western hemlock is also primarily found west of the Cascades and is a common associate with Douglas-fir. It is very shade-tolerant and establishes in the understory of natural or planted Douglas-fir stands (Minore, 1979). Initial growth is slow, but trees will eventually become co-dominant in the overstory if allowed enough time to develop. Noble fir is a subalpine species that occurs primarily in the Cascades at elevations of ~700 – 1650 m. The species has intermediate shade tolerance but grows best in full sunlight; relative to Douglas-fir, initial juvenile growth is generally slow, but total stand volume can be much higher over time (Cope, 1993). Noble fir is a common associate with Douglas-fir but is also found in pure stands. Western white pine is found throughout the PNW region, including in the Cascades and throughout western Washington across a wide range of elevations. The species is classed as having intermediate shade tolerance and establishes well under partial shade but grows best in full sunlight after establishment (Graham, 1990). Western white pine occurs in a variety of cover types, co-occurring with some of the true firs, ponderosa pine, lodgepole pine (*Pinus contorta),* Douglas-fir, western hemlock, western redcedar, and others. Across its range, western white pine has experienced widespread mortality via white pine blister rust (*Cronartium ribicola*), significantly influencing the dominance of this species in the region (Tomback and Achuff, 2010).

2.3. Experimental design and measurements

Each trial was installed as a separate completely randomized design at experimental areas within 2 km of each other. Each trial consisted of three treatments: a mixture containing an equal mix of DF with one of the three species assessed (either WH, NF, or WWP), pure plantings of DF only, and pure plantings of the other component species. All treatments were applied to square plots 0.4 ha in size, but the number of replications varied depending on the trial. For the WH trial, there were four replications each of the mixture and pure WH treatments, and 10 replications of the pure DF treatment. For the NF trial, there were three replications each of the mixture and pure DF treatments, and four replications of the pure NF treatment. For the WWP trial, there were three replications each of the mixture and pure DF treatments, and six replications of the pure WWP treatment. Variation in the number of replications exist because planned manipulations in some of the plots did not occur (Erickson et al., 2009). Replications in each trial were adjacent to each other with the exception of the NF trial where the experimental area was bisected by a forest road. The NF trial was planted in 1980, the WH trial in 1981, and the WWP in 1982; planting occurred in the spring with 2 year old bare root stock planted at a square spacing of 3 m. Mixed plots were planted so that each tree was surrounded by trees of the other component species. DF and WH seed were sourced from local populations at approximately 610 m elevation, NF from a 910 m seed source, and WWP seed was sourced from apparently blister rust-resistant mother trees located between 760 and 1070 m.

Measurements were conducted on tagged trees located in permanent plots that were established in 1989 (7 – 9 years after planting). Measurement plots encompassed the internal grid of 14 × 14 trees (196 trees total) in the treatment plot. Measurements were conducted periodically throughout the study duration, most recently in fall 2021, following diameter growth cessation of that year (corresponding to 41, 40, and 39 growing seasons since planting for NF, WH, and WWP trials, respectively). Trees were recorded as alive or dead, all live trees were measured for diameter at breast height (DBH, 1.3 m; precision of 0.1 cm), and a subset of trees (~40 – 60 per plot) were measured for 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.

2.4. Data analysis

We limited our analysis to the data collected from the most recent measurement period in 2021. Each trial was analyzed independently for all analyses including using only the pure DF plots associated with a given trial. Plot means were calculated using originally planted trees only for the following variables: relative survival (as a proportion) of originally planted trees, quadratic mean diameter (cm), mean height for trees measured for height only (m), live basal area (m^2 ha^{-1}), total (live) wood volume (m^3 ha^{-1}). For mixed-species plots, we also calculated these variables for each of the component species to assess their contribution to the overall plot mean. For all plots, we calculated height to diameter ratios (H:D) of planted trees (using only trees with measured heights) and calculated separate H:D for each component species for the mixture plots. We also calculated total wood volume and Reineke's Stand Density Index (SDI, Reineke, 1933) for all live trees (planted + ingrowth) > 4 cm DBH. For live tree 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. Individual tree volumes were then calculated using published equations for DF (Bruce and DeMars, 1974), WH (Wiley et al., 1978 as cited in Hoyer and Swanzy, 1986), NF (Browne, 1962), and WWP (Wykoff et al., 1982), and then summed within a measurement plot to estimate total wood volume per ha.

We fit trial-specific generalized linear models to assess the effect of planting composition in the most recent measurement (stand ages since planting of 39 – 41 years) for each of the following plot-level response variables: relative survival (as a proportion of those planted), quadratic mean diameter (QMD), mean tree height, live basal area, total wood volume of live, originally planted trees, SDI, and total wood volume of all live trees > 4 cm DBH. For each trial and response variable, we fit a model that included the categorical predictor of composition with three levels (e.g., mixture of DF and companion species, pure stand DF, pure stand companion species). Models of relative survival were fit with a beta distribution and logit link, as appropriate for proportion data. The remaining models were fit with both Gaussian and gamma distributions; the form that best met model assumptions of residual distribution was used for interpretation. Models of QMD, mean tree height, and live basal area were fit with a Gaussian distribution, and models of SDI were fit with a gamma distribution and log link. Models of total wood volume of live, originally planted trees and all live trees > 4 cm DBH were fit with a gamma distribution and log link except for volume of planted trees in the NF trial, which was fit with a Gaussian distribution. We assessed composition effects on individual height to diameter ratios separately for each trial by species combination. For each trial and species, we fit a generalized linear mixed model that included the categorical predictor of composition with two levels (pure stand vs. mixture) and a random effect of plot. Models of height to diameter ratio were fit with a Gaussian distribution, except for Douglas-fir in the WH trial, which was fit with a gamma distribution and log link.

Statistical analyses were conducted in R version 4.4.0 (R Core Team, 2024). All models were fit with *glmmTMB* (Brooks et al., 2017). Prior to interpretation, models were evaluated for outliers and uniform residuals with *DHARMa* (Hartig, 2021). We used an alpha level of 0.10 to account for low replication in some treatments and high inherent variability within natural systems to reduce the likelihood of a Type 2 error. When model results indicated significant treatment effects, we conducted preplanned contrasts between the mixture and each of its respective components with *emmeans* (Lenth, 2024). Results were visualized with *ggplot2* (Wickham, 2016) and *patchwork* (Pedersen, 2024).

3. Results

3.1. Douglas-fir – western hemlock mixture

There was a significant effect of treatment in the DF-WH trial on relative survival, quadratic mean diameter (QMD), mean height, total wood volume, and live basal area for originally planted trees (i.e., not considering ingrowth) (Table 1). However, when evaluating contrasts between the mixture and each monoculture treatment, differences were only significant for relative survival, QMD, and mean height. Both

Table 1
Analysis of deviance test statistics for effects of mixture treatments for each species trial on relative (proportional) survival, quadratic mean diameter, mean tree height, total wood volume, and live basal area for originally planted trees only, and for stand density index (SDI) calculated from both planted and ingrowth trees. DF = Douglas-fir, WH = western hemlock, NF = noble fir, WWP = western white pine.

	DF – WH trial		DF – NF trial		DF – WWP trial	
Response variable	Chi-square	P value	Chi-square	P value	Chi-square	P value
Relative survival	9.85	0.007	0.44	0.803	17.02	<0.001
Quadratic mean diameter	10.90	0.004	12.88	0.002	0.67	0.714
Mean height	26.84	<0.001	17.83	<0.001	4.35	0.114
Total wood volume	7.37	0.025	7.59	0.022	33.28	<0.001
Live basal area	4.80	0.091	5.82	0.062	32.81	<0.001
Stand density index	0.75	0.687	0.50	0.778	28.73	<0.001

monoculture treatments had higher relative survival (by 0.13) compared to the mixture treatment (Fig. 1a, Table 2), and a majority of the survival in the mixture was comprised of DF (Fig. 1a). The pure WH treatment had significantly lower QMD (-3.3 cm, 90 % CI: −4.9, −1.6) and mean height (-4.0 m, 90 % CI: −5.9, −2.1) than the mixture, apparently due to greater QMD and height of DF in the mixture compared to the DF monoculture (Fig. 1b-c). There was no difference in total wood volume of planted trees between the mixture and each of the monocultures ($p = 0.158$; Fig. 1d). Ingrowth in the DF-WH trials occurred throughout stand development with no striking differences among treatments in diameter distributions (Figure S1, Supplementary Materials). When including ingrowth, there were no significant differences in stand density index (SDI, $p = 0.687$; Table S1, Supplementary Materials) or total wood volume ($p = 0.218$; Figure S2, Supplementary Materials).

3.2. Douglas-fir – noble fir mixture

In the DF-NF trial, there were significant effects of treatment on QMD, mean height, total wood volume, and live basal area for originally planted trees (Table 1). Treatment effects were consistent and manifested as higher values in the mixture compared to the NF monoculture (Table 2), which were driven by greater contributions of DF to stand growth in the mixture associated with greater survival (Fig. 2a), QMD (Fig. 2b), and mean height (Fig. 2c). The DF monoculture differed from the mixture only with respect to mean height, which was 5.6 m greater (90 % CI: 0.3, 10.8) in the monoculture than in the mixture (Fig. 2c). Relative survival was similar across treatments (mean values ranged from 0.59 to 0.63, Table S1, Supplementary Materials), but the proportion survival of DF was greater than that of NF in the mixture (Fig. 2a). The diameter distribution of ingrowth trees indicates similar levels of recruitment of smaller size classes across all treatments in the DF-NF trial (Figure S1, Supplementary Materials). This was reflected in findings of no difference in SDI (Table 1) or total wood volume of all trees among treatments ($p = 0.253$); the pattern of total wood volume was similar when considering original planted trees or when including ingrowth (Figure S2, Supplementary Materials).

3.3. Douglas-fir – western white pine mixture

In the DF-WWP trial, there were significant treatment effects on relative survival, live basal area, and total wood volume for originally planted trees (Table 1). Effects manifested as significantly higher values in the DF monoculture relative to the mixture, and significantly lower values in the WWP monoculture relative to the mixture (Fig. 3a and 3d, Table 2). Differences in total wood volume between the mixture and monocultures (estimated as 52 m^3 ha^{-1} greater and 66 m^3 ha^{-1} less than the mixture for the DF and WWP monocultures, respectively) were driven by differences in survival, as disparities in QMD and mean height of WWP and DF in the mixture were small (Fig. 3b-c). When including ingrowth, the same finding was observed for total wood volume (Figure S2, Supplementary Materials) and SDI; SDI was greater in the DF monoculture relative to the mixture, and lower in the WWP monoculture relative to the mixture (Table S1, Supplementary Materials). Diameter distributions in each treatment indicate variation in recruitment across treatments with the greatest representation of smaller size classes in the WWP monoculture, followed by the mixture, and relatively few in the

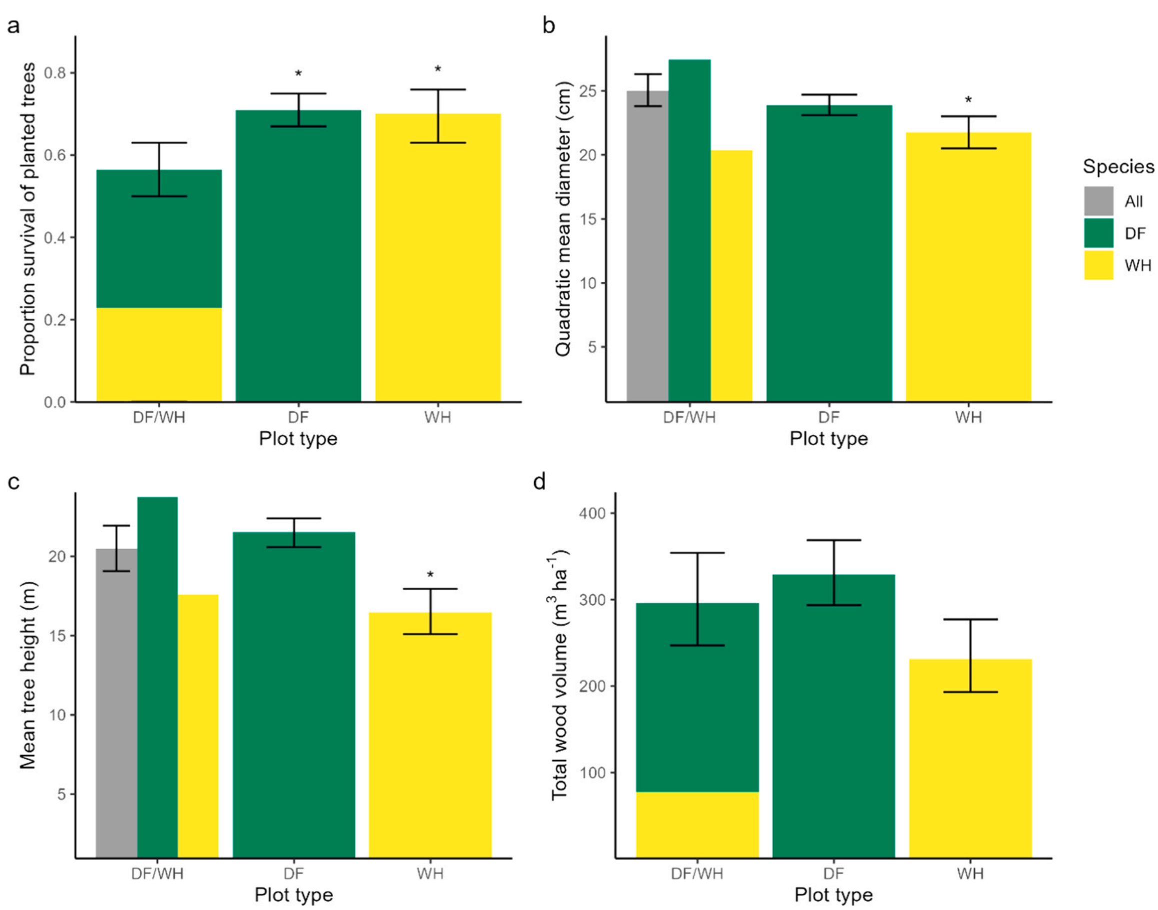

Fig. 1. Mean responses of Douglas-fir-western hemlock mixture and monocultures of each component species for relative (proportional) survival of planted trees (a), quadratic mean diameter (b), mean tree height (c), and total wood volume (d). Mixture values are presented to show the contribution of each species to the overall value. Asterisks above a species indicate a significant difference ($P < 0.1$) between that component species monoculture and the mixture. All values were calculated using originally planted trees only. Error bars are 90 % confidence interval of the overall mean. DF = Douglas-fir, WH = western hemlock.

Table 2
Significant contrast estimates between a given mixture and pure stands of each of its component species for relative (proportional) survival, quadratic mean diameter, mean height, total wood volume, and live basal area for originally planted trees only. Response variables not shown were not significantly different among treatments. Values in parenthesis are 90 % confidence interval of the mean or estimated difference.

Response variable	Mixture mean value (90 % CI)	Douglas-fir difference from mixture	Companion species difference from mixture
Douglas-fir – western hemlock			
Relative survival	0.57 (0.5, 0.63)	0.14	0.13
Quadratic diameter (cm)	25.0 (23.9, 26.2)	−1.2 (−2.6, 0.2)	−3.3 (−4.9, −1.6)
Mean height (m)	20.5 (19.1, 21.9)	1.0 (−0.6, 2.6)	−4.0 (−5.9, −2.1)
Douglas-fir – noble fir			
Quadratic diameter (cm)	29.2 (25.3, 33.2)	1.5 (−4.2, 7.1)	−8.9 (−14.1, −3.6)
Mean height (m)	20.1 (16.3, 23.8)	5.6 (0.3, 10.8)	−7.0 (−11.9, −2.1)
Total wood volume (m^3 ha^{-1})	414 (290, 539)	79 (−98, 255)	−186 (−350, −21)
Live basal area (m^2 ha^{-1})	45 (33, 57)	3 (−14, 20)	−17 (−33, −2)
Douglas-fir – western white pine			
Relative survival	0.63 (0.56, 0.70)	0.12	−0.09
Total wood volume (m^3 ha^{-1})	331 (303, 362)	52 (7, 103)	−66 (−93, −36)
Live basal area (m^2 ha^{-1})	36 (34, 38)	4 (0.5, 7)	−6 (−9, −3)

DF monoculture (Figure S1, Supplementary Materials).

3.4. Height to diameter ratios across trials

The response of height to diameter (H:D) ratios was consistent across trials. Douglas-fir H:D was significantly lower when grown in a mixture with WH, NF, or WWP compared to when it was grown as a monoculture (Table 3). The opposite pattern was observed for the companion species; H:D was significantly greater for WH, NF, and WWP when grown in a mixture with DF compared to when each was grown as a monoculture (Table 3).

4. Discussion

Planting mixed-species stands may provide additional benefits relative to monocultures, but the practice is not commonly used operationally in the PNW region. This is partially a result of the relative ease with which monocultures can be managed relative to mixtures but is also due to insufficient information on long-term responses of planted mixed-species stands. Our study provides one of the longest experimental assessments for mixed-species stands of Douglas-fir, a commercially and ecologically important tree species in the PNW region. In general, our findings indicate that Douglas-fir dominates growth dynamics when grown in a mixture, with higher survival (relative to the companion species in the mixture) and greater height and diameter growth (relative to monocultures) that results in large contributions to total stand basal area and wood volume. Importantly, there was little evidence of complementary effects; monocultures of Douglas-fir generally had higher total wood volume compared to the mixtures (but only significant for the WWP-DF trial) at this time in stand development.

Douglas-fir performed better than each companion species whether grown in pure stands or in a mixture. This was not surprising as rapid juvenile growth coupled with the development of high live crown ratios allows Douglas-fir to outcompete other species and dominate stand productivity (Hermann and Lavender, 1999; Talbert and Marshall, 2005). The effect of mixing on Douglas-fir H:D ratios reflects this dynamic, as lower ratios in all mixture treatments indicate lower interspecific competition for light compared to monoculture stands where intraspecific competition is high. Erickson et al. (2009) reported the same response for the WH-DF trial at year 24, but there was no difference in H:D for the WWP-DF trial at year 20. The delayed H:D response in the WWP-DF trials may be a result of the similar shade tolerance of these two species (Minore, 1979), causing both to allocate more resources to height growth to compete for light during earlier stand development. Regardless, it appears Douglas-fir gained light dominance in WWP-DF prior to the most recent measurement (stand age 39 years), and also in the DF-NF trial at some point in stand development. Given the consistency across trials and findings from other studies (see below), it seems likely that that this response would occur in most situations for Douglas-fir mixtures with other native conifer species west of the Cascade crest.

The lack of complementary effects on total wood volume (i.e., overyielding) was reported at earlier periods of the study (Erickson et al., 2009) and in other studies evaluating Douglas-fir mixtures with shade-tolerant species including western redcedar (Omari et al., 2021) and western hemlock (Himes and Puettmann, 2020; Amoroso and Turnblom, 2006). The null response has also been found in other mixture trials in the PNW with species other than Douglas-fir that spanned a range of shade tolerance (Chen and Klinka, 2003; Garber and Maguire, 2004; Maguire and Mainwaring, 2021). These findings contrast with a recent meta-analysis that reported higher yield in mixtures compared to monocultures across a global dataset (Feng et al., 2022). Forrester et al. (2005) highlighted the importance of selecting species that complement each other in shade tolerance and growth rates that allow the shade-intolerant species to attain dominance in the overstory. Given this, the lack of complementary effects in the WWP-DF and NF-DF mixtures is not surprising given the similar levels of shade tolerance among those species, where competition for light resulted in suppression of western white pine and noble fir at the expense of enhanced Douglas-fir growth.

For the WH-DF trial, the absence of a complementary volume response in the mixture was somewhat surprising given the contrasts in shade tolerance and growth rates between the two species. These species commonly co-occur in the PNW (Franklin and Dyrness, 1973), forming a stratified canopy that increases light interception (Wierman and Oliver, 1979; Pretzsch, 2014). The finding is at least partly due to higher mortality in the WH-DF mixture compared to the pure WH and DF treatments (Fig. 1a), as noted by Erickson et al. (2009). They calculated relative yield of individual Douglas-fir trees in the mixture to be higher relative to pure stands, indicating potential for greater productivity in the mixture if tree survival was comparable to that of the pure stands (Erickson et al., 2009). This trend appears to have continued given the species' differences in QMD and mean height between mixtures and monocultures in this measurement (Fig. 2b-c), but the effect was not large enough to compensate for lower survival and its effects on total wood volume growth (Fig. 2a and 2d). We do not have any definitive information on what caused the higher mortality in the mixture but assume it is a treatment effect that occurs when growing western hemlock and Douglas-fir in mixture. Note that when all trees are included in the analysis (planted + ingrowth), total volume was numerically higher in the mixture (by ~6 %, statistically non-significant) compared to the pure stand, demonstrating the potential for greater stand yield in WH-DF mixtures over time. Amoroso and Turnblom (2006) found comparable productivity between WH-DF mixtures and DF monoculture at age 12, but only at a high planting density (1729 trees per hectare [TPH]). High planting densities are known to accelerate stand development (Assman, 1970; DeBell et al., 1997; Harrington et al., 2009) and have been shown to influence the timing and magnitude of overyielding (Maguire and Mainwaring, 2021). The lower (but more operationally relevant) planting density in our trial (1111 TPH) coupled with higher mortality

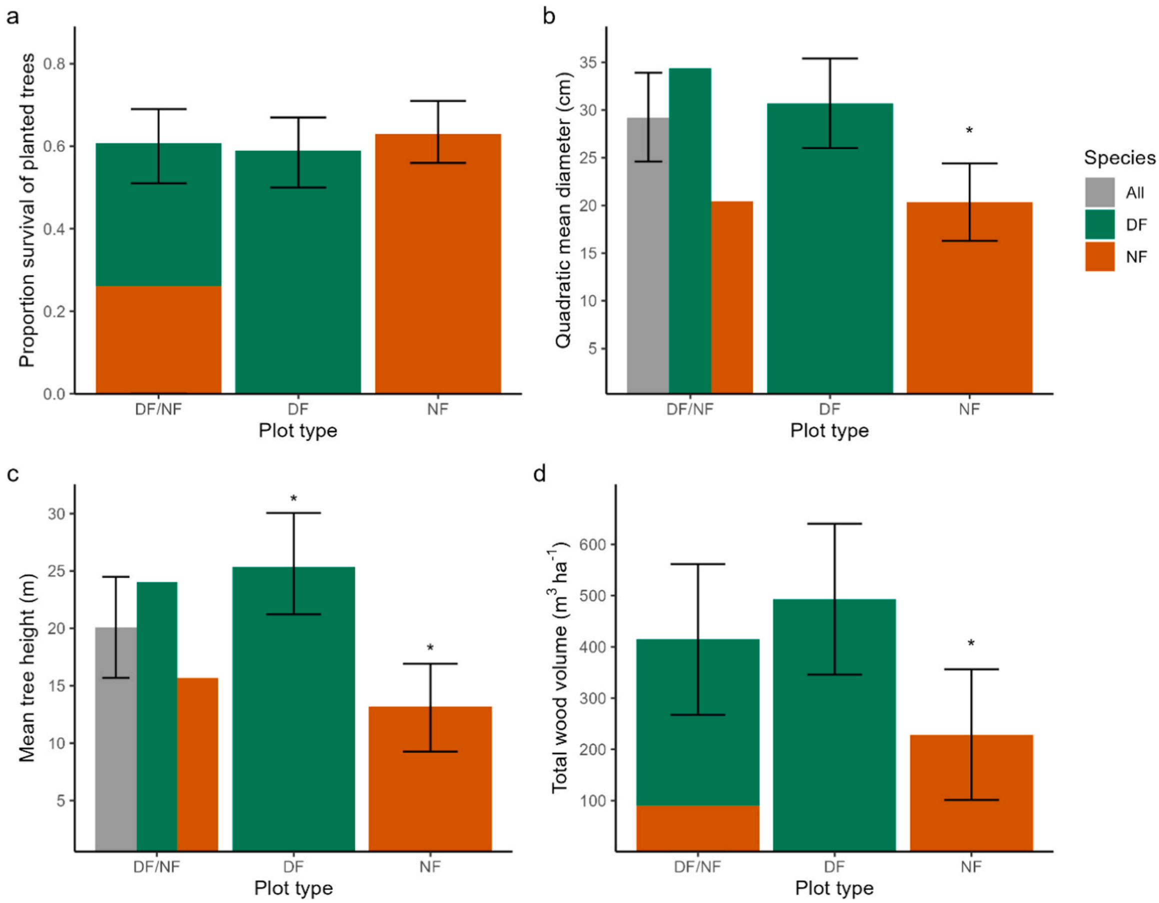

Fig. 2. Mean responses of Douglas-fir-noble fir mixture and monocultures of each component species for relative (proportional) survival of planted trees (a), quadratic mean diameter (b), mean tree height (c), and total wood volume (d). Mixture values are presented to show the contribution of each species to the overall value. Asterisks above a species indicate a significant difference ($P < 0.1$) between that component species monoculture and the mixture. All values were calculated using originally planted trees only. Error bars are 90 % confidence interval of the overall mean. DF = Douglas-fir, NF = noble fir.

has likely delayed the onset of complementary effects in the WH-DF trial. We expect that overyielding will eventually occur if stand development continues in the absence of disturbance.

The increased growth of Douglas-fir trees in a mixture compared to a monoculture is similar to the well-known effect of planting density on growth metrics, where lower density stands have higher individual tree growth but lower total stand volume until later stages of stand development (Gabira et al., 2023; Harrington et al., 2009; Reukema and Smith, 1987). This appears to be the case here, as Douglas-fir trees grown in a mixture were larger regardless of the species they were mixed with, similar to responses observed at this site when planting at low densities (~300 – 400 TPH, Slesak et al., 2025). This has important management implications, as Douglas-fir managed for fiber production is often precommercially thinned (PCT) during the second decade after planting to avoid competition-induced mortality and increase stand productivity (Curtis, 2006). Planting Douglas-fir in a mixture could avoid the need for PCT (Wierman and Oliver, 1979), while achieving additional benefits associated with mixtures. Given the consistency of this response across trials, it is likely that this dynamic would occur when planting Douglas-fir with other common co-occurring conifer species.

The potential for greater stand productivity is only one possible benefit of planting mixed-species stands and depending on objectives, it may not be a major factor when choosing what to plant. Benefits of mixtures are varied and include reduced vulnerability to extreme climate and forest health stressors, increased biodiversity and habitat (arising from greater structural complexity; e.g., Himes and Puettmann, 2020), increased carbon storage (Warner et al., 2023), and greater market flexibility (Liu et al., 2018; Carnol et al., 2014; Messier et al., 2022). Using dendrochronology at the same trials assessed here, Byassee (2024) determined that the Douglas-fir grown in a mixture responded more favorably to stressful heat and drought events than those grown in a monoculture. The possibility of increased resilience to extreme weather events may be an important factor landowners consider when planning reforestation activities given the greater frequency at which these events are occurring (Heeter et al., 2023).

4.1. Limitations and inference

A limitation of the study was the occurrence of ingrowth in each of the trials (Figure S1, Supplementary Materials). Ingrowth in long-term silvicultural studies is to be expected unless continuously controlled, but some that was observed here occurred in the largest size classes, making it likely that it established early in the study. Tree density influences all aspects of stand development (Slesak et al., 2025), and the presence of significant ingrowth over the course of the study could have masked or modified apparent effects of mixing on stand characteristics and the potential for overyielding. In particular, ingrowth in the WH-DF and the WH monocultures increased total wood volume by 20 % and 23 %, respectively, compared to the total wood volume of planted trees only; ingrowth in the other trials was comparatively small (Figure S2, Supplementary Materials). Further examination of ingrowth in the western hemlock trial indicated that it was comprised almost entirely of Douglas-fir and western hemlock, with the former in larger size classes and the latter in smaller size classes (data not shown). It is difficult to evaluate if our findings based on planted trees would have differed with

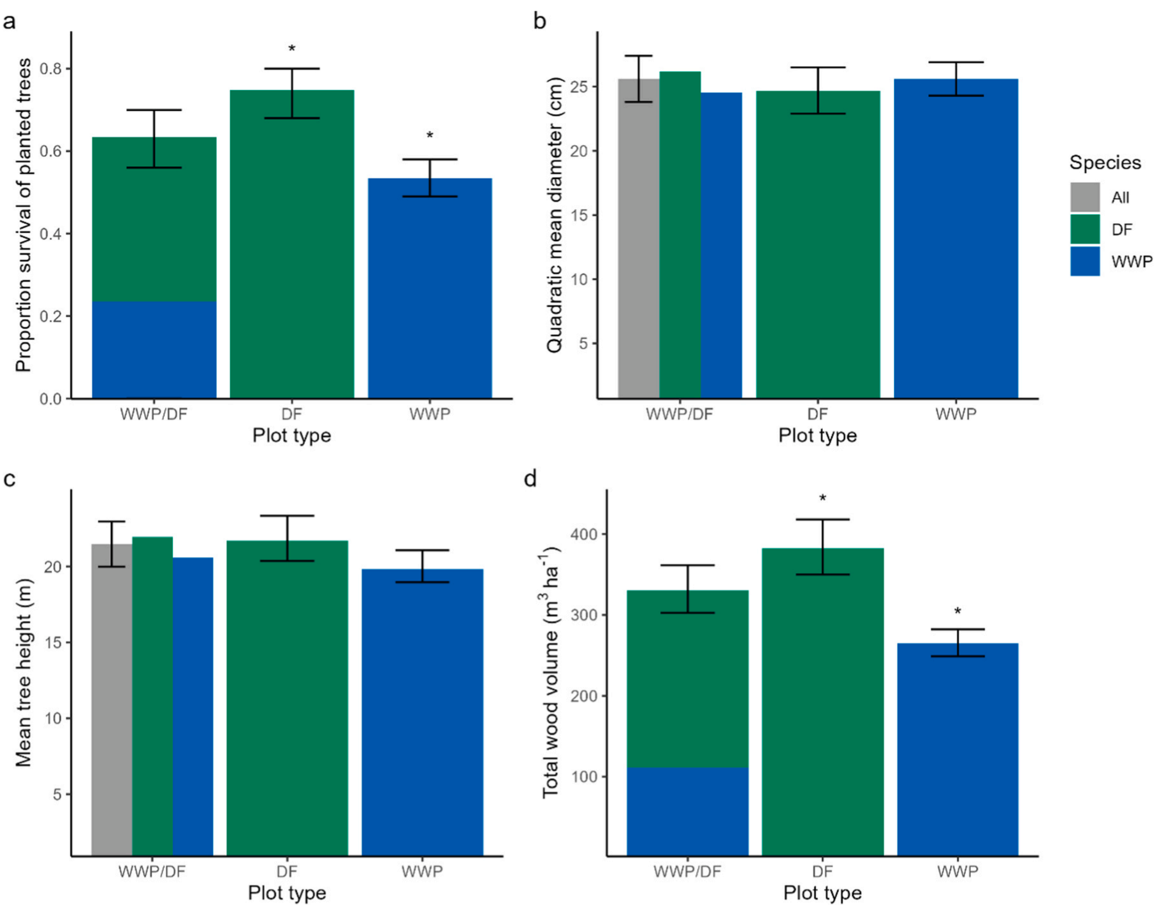

Fig. 3. Mean responses of Douglas-fir-western white pine mixture and monocultures of each component species for relative (proportional) survival of planted trees (a), quadratic mean diameter (b), mean tree height (c), and total wood volume (d). Mixture values are presented to show the contribution of each species to the overall value. Asterisks above a species indicate a significant difference ($P < 0.1$) between that component species monoculture and the mixture. All values were calculated using originally planted trees only. Error bars are 90 % confidence interval of the overall mean. DF = Douglas-fir, WWP = western white pine.

Table 3
Comparison of mean height to diameter (H:D) ratios for Douglas-fir and the companion species for each trial when grown in a mixture or pure monoculture. Associated p values for each comparison are listed; values in parenthesis are 90 % confidence limits of the mean. DF = Douglas-fir, WH = western hemlock, NF = noble fir, WWP = western white pine.

Associated Trial	DF in mixture	DF in monoculture	P value DF	Companion in mixture	Companion in monoculture	P value companion
DF-WH	84 (81, 87)	91 (89, 93)	0.006	87 (83, 91)	77 (74, 81)	0.002
DF-NF	70 (67, 73)	81 (78, 84)	<0.001	80 (72, 88)	65 (58, 72)	0.016
DF-WWP	84 (83, 86)	93 (92, 95)	<0.001	88 (84, 91)	81 (79, 84)	0.023

lower amounts of ingrowth. Given the similarity in SDI (which includes ingrowth) between the WH-DF mixture and the DF monoculture (Table S1, Supplementary Materials), density-dependent effects on stand growth would have been similar between these treatments, providing further evidence that the higher (non-significant) total wood volume in the WH-DF mixture indicates the occurrence of overyielding in that treatment. Ingrowth is common in operational management, and its effect on inference of our findings will be dependent on how managers typically address it in stand development (e.g., removal during PCT vs. retention until final harvest).

Given that these trials occurred in close proximity on similar soils and climate, the role of site quality on the responses we report cannot be quantified. Our site is of moderate productivity (Curtis et al., 2016), and results at lower or higher quality sites may differ. For example, Jactel et al. (2018), using meta-analysis on a global dataset, reported that the effect of overyielding increased with increasing precipitation. Effects of species mixtures are likely to vary with site conditions such as local climate, but similar findings of other studies evaluating Douglas-fir mixtures in this region (Amoroso and Turnblom, 2006; Himes and Puettmann, 2020; Omari et al., 2021) suggest that our general findings regarding Douglas-fir may be broadly applicable.

As with all research studies, the relevance of our findings to management is dependent on how well the experimental conditions align with operational practice. Intermediate treatments, such as precommercial and commercial thinning, can influence total yield (Weiskittel et al., 2011; Bose et al., 2018) but were not incorporated into our design as they would have confounded interpretation of any mixing effects on overyielding (Pretzsch et al., 2019). As a result, treatment effects on potential merchantable volume yielded over the course of a rotation is not clear, possibly limiting utility of the findings for some management regimes. However, the use of thinning (both precommercial and commercial) in the PNW region is becoming less common because of the high cost of thinning in the western U.S. (Chang et al., 2023), limited resources for implementation on federal ownerships (North et al., 2019), and/or a shift in objectives that no longer emphasizes maximum wood production. Given this, our findings may have broad inference for contemporary forest management across the PNW region.

5. Conclusion

Planting Doulgas-fir in mixtures with the other common co-occurring conifer species assessed here does not result in complementary effects to total stand productivity over rotation length time periods. In the absence of disturbance, it is possible that such an effect would manifest in the WH-DF mixture at some point in the future as the shade-tolerant western hemlock component continues to develop. Given our findings and those of others, we conclude that Doulgas-fir is likely to dominate in many planted conifer mixtures via greater survival and growth relative to the other species in the mixture. Mixing consistently increased Douglas-fir growth, resulting in larger individual trees relative to those grown in monocultures. The effect has important implications for stand development and the need for intermediate treatments such as precommercial thinning. Managers can use this information to make informed decisions on the utility of using species mixtures to achieve their specific management objectives.

CRediT authorship contribution statement

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

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.2025.123141.

Data availability

Data will be made available on request.

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