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Coast redwood planted outside its range outperforms the native Douglas-fir beneath an overstory of varying density

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Restoration of conifer dominance and structural complexity in second-growth forests of northern California is a key management objective following historic logging and fire exclusion. We evaluated the performance of coast redwood (*Sequoia sempervirens*) and coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) nursery stock 8 years after planting following a retention harvest designed to enhance fine-scale heterogeneity in the spatial pattern of overstory tree retention. The study was conducted just outside redwood's range in Humboldt County, north coastal California. Redwood exhibited higher survivorship over 8 years since planting, and had the same average height as Douglas-fir after 8 years, growing more rapidly and catching up in height over the last 2 years. Douglas-fir mortality was greater in areas of higher overstory retention. Canopy openness and soil relative water content were the strongest predictors of height and recent height increment. These early findings indicate that redwood can establish and perform competitively outside its natural range under the retention system, supporting potential expansion of its use in timber production and for other objectives such as wildfire resilience, carbon sequestration, structural complexity, and biodiversity enhancement. Continued monitoring will be essential to determine how varying retention levels and soil moisture dynamics influence the long-term development of planted conifers under a spatially-heterogeneous canopy.

KEYWORDS
assisted migration, forest restoration, multiaged silviculture, *Pseudotsuga menziesii*, *Sequoia sempervirens*, variable retention, variable-density thinning

Introduction

Promoting dominance of merchantable, fire-resistant conifers such as coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and redwood (*Sequoia sempervirens*) is a common forest management objective in the coastal Pacific Northwest, USA, particularly in northern California. Tanoak (*Notholithocarpus densiflorus*) is the most common hardwood associate of redwood in central and southern portions of its range and most abundant across redwood forests (Tappeiner et al., 1990; Sawyer et al., 2000). After historic logging or wildfire disturbances gave rise to second-growth stands, tanoaks commonly resprouted

from established root systems (Ramage et al., 2010). This competitive advantage of rapidly sprouting hardwoods with established root systems over conifers that can be slow to establish, can lead to poor survival and slow early growth of regenerating conifers (Harrington et al., 1991; Harrington and Tappeiner, 1997, 2009; Schneider et al., 2023). Commonly, spatially-variable survival and growth of regenerating conifers have led to development of second-growth stands comprising a mosaic of patches dominated by either conifer or hardwood (Berrill et al., 2017).

Restoring structural complexity within second growth stands of the Pacific Northwest has become an important management objective in recent years (Donato et al., 2012; Franklin and Johnson, 2012; Willis et al., 2021). An increasingly popular forest restoration strategy is variable-density thinning (VDT), an intermediate treatment that enhances structural heterogeneity by prescribing different retention levels across a stand (Carey, 2003; O'Hara et al., 2012). In redwood forests of northern California, VDT is a key restoration tool for accelerating the development of historic forest structure in even-aged stands (O'Hara et al., 2012). By creating a mosaic of harvest gaps, thinned areas, and unharvested "skips," VDT promotes heterogenous stand structural conditions characteristic of old growth redwood forests (Harrington et al., 2005; Dagley et al., 2018; Soland et al., 2021).

The retention system, also referred to as variable retention (VR) is a multiaged regeneration method that intentionally retains structural elements of a mature forest (large trees, snags, logs) and regenerates a new cohort of trees to achieve various objectives (Franklin et al., 1997; Helms, 1998; Mitchell and Beese, 2002). VR can be implemented using aggregated and/or dispersed patterns, and is typically implemented across large areas and can result in large patches of similar retention density rather than fine-scale variability. To enhance spatial variability and tree-size heterogeneity, Berrill et al. (2018) developed a new variant of VR named variable-density retention (VDR). VDR combines the retention of key structural elements like VR, plus the fine-scale spatial heterogeneity created by VDT. Berrill et al. (2018) demonstrated that by applying deliberate variation in harvest intensity throughout the stand while retaining structural elements desired to meet owner management objectives such as timber production, structural complexity, biodiversity, and ecological function. Simultaneously, the retention harvest liberated growing space for a new cohort of redwood and Douglas-fir growing under a variable canopy.

The natural range of redwood is restricted to a narrow coastal strip extending from southwestern Oregon to southern Monterey County, California, where redwoods benefit from moderate temperatures and abundant summer fog (Olson et al., 1990). There is widespread interest in growing redwood inside and outside its natural range due to several of its appealing characteristics. For example, it has few pest or disease issues, and the wood is highly valued for its heartwood coloration and decay resistance. Redwood is also known for its rapid growth and carbon sequestration (Watt and Kimberley, 2022), and has been successfully established far outside its range in countries including New Zealand (Rapley, 2018), Germany (Breidenbach et al., 2020), and France (Arnaud et al., 1993). Coast Douglas-fir has a broader ecological amplitude than redwood, with a natural range extending from British Columbia, Canada down through Washington and Oregon to Santa Barbara County in southern California, and further inland into California's Klamath Mountains and Sierra Nevada Mountains (Hermann and Lavender, 1990).

Successful regeneration of Douglas-fir and redwood is influenced by species-specific ecological requirements. Douglas-fir regenerates from seed and often best establishes under open canopy conditions and is sensitive to competition from hardwoods and dense understory vegetation (Hermann and Lavender, 1990; Harrington et al., 1991). Redwood is more shade tolerant than Douglas-fir and regenerates both from seed and vegetatively via stump sprouts and basal sprouts (Neal, 1967; Olson et al., 1990).

In this study, we applied VDR in a mixed hardwood-conifer stand dominated by tanoak that was initiated by clearcutting and regenerated naturally. Our objectives were to shift stand composition back to conifer dominance and evaluate performance of planted redwood and Douglas-fir. Because Douglas-fir is generally more light demanding, while redwood is more tolerant of shade, we expected their performance to differ in response to site conditions such as canopy cover, soil moisture, and surrounding vegetation. Here we examine and report on planted conifer growth over the 8 years since planting, seeking to: (1) identify biophysical factors linked to understory performance, and (2) quantify early growth of each species and variability in growth of the new cohort which may be desirable when seeking to enhance structural complexity in terms of tree-size variability.

Materials and methods

This analysis is part of a larger study that builds upon previous work by Berrill et al. (2018) and Kerhoulas et al. (2020). Our study site was located at L.W. Schatz Demonstration Tree Farm (40° 46′ 30.306″ N, −123° 51′ 58.036″ W), approximately 29 km inland from the Pacific coast and 14 km southeast of Korbel, California in Humboldt County. This site is located just outside the coastal fog belt and the natural range of redwood. It lies at 160 m elevation and has a mean annual rainfall of 1,450 mm. The Mediterranean climate results in warm, dry summers. The typical temperature range varies from 4 °C to 18 °C annually, and is more extreme than the mild coastal temperature redwood is used to, often only ranging from 10 °C to 15 °C.

The site was historically dominated by Douglas-fir. Around 1960, the original stand was harvested, initiating natural regeneration of sprouting hardwoods, mainly tanoak and California bay (*Umbellularia californica*), and conifer seedlings, mainly Douglas-fir and grand fir (*Abies grandis*), supplemented in some places with planted Douglas-fir. The understory mainly comprised shade-tolerant species: sword fern (*Polystichum munitum*), redwood sorrel (*Oxalis oregana*), evergreen huckleberry (*Vaccinium ovatum*), and poison oak (*Toxicodendron diversilobum*) (Berrill et al., 2018).

The 0.6 ha (6,000 m^2) study site was divided into three slope position blocks oriented east-west (upper, middle, lower), each subdivided into five 20 m × 20 m (0.04 ha) square patches. One of five treatments was randomly assigned to each patch: clear gap, low-, medium-, high density retention, or uncut "skip" treatment. Gap treatments removed all trees. Thinning treatments retained primarily conifers, and reduced stand density index (SDI; metric) to 225, 450, or 675 for the low, medium, and high retention levels,

respectively. These levels of retention are equivalent to 15%, 30%, and 45% of the upper limit of Douglas-fir SDI (1500; Reineke, 1933). Uncut patches had variation in stocking (1000, 1050, and 1600 SDI) (Berrill et al., 2018).

During the autumn of 2014, trees marked for removal in treatment patches were harvested. We retained some hardwood tops and limbs, along with a few large conifer logs per block as coarse woody debris. The following spring 2015, 1-year-old Douglas-fir and redwood grown in Styro-15 containers from a local nursery were planted by hand in an intimate mixture at approximately 3 m spacing and also 3 m from residual trees, resulting in planted understory density of approximately ~875 stems/ha^{-1} or 35 conifers per harvested patch. Some placement of planted conifers was adjusted to avoid hardwood stumps or for selection of best microsite. Planted conifer locations were mapped, and their height was measured at time of planting, then re-measured at years two (2016) and three (2017). At each census, evidence of animal browsing to the leader shoot was recorded.

In October 2017, three growing seasons after planting, immediately prior to the first winter rainfall at the end of the dry summer growing season, soil relative water content (RWC) was measured at each redwood and Douglas-fir. FieldScout TDR 300 probes (20 cm rods) were used, calibrated against local silt loam reference sample with field capacity and permanent wilting point of 35% and 18% volumetric water content, respectively. Two measurements were taken within 20 cm of the stem and averaged. Basal area in the vicinity of each planted conifer was assessed using a variable-radius plot with 9.19 m^2/ha^{-1} prism (40-factor English unit prism) centered upon each conifer. We quantified re-sprouting hardwood competition by counting re-sprouting stumps within 2.5 m of each seedling. Percent cover of understory vegetation and ferns was estimated within 1 m^2 quadrats centered on each seedling, with ferns assessed separately due to their distinct growth form and potential competitive effects. Canopy cover/openness and understory light over the growing season were estimated using hemispherical photographs taken above each conifer on overcast days. Images were analyzed in Gap Light Analyzer 2.0 (Frazer et al., 1999), assuming 0.75 cloudiness index, growing season of April to September, and using a custom topographic mask derived from clinometer readings every 10° azimuth (Berrill et al., 2018). In addition to these early measurements, conifers were re-measured for height in 2021 after 6 years on site, and in 2023 after 8 years on site, to assess survival and height growth, and record instances of damage such as broken tops that were expected to impact height development.

Analysis

Our analysis focused on studying relationships between total height or recent height growth of planted trees and biophysical factors. Therefore, any planted conifers that sustained top damage causing reduced height growth were excluded from the analysis, resulting in 197 trees being included. Data for total height and height increment were transformed to reduce skewness, which was best accomplished by square root transformation. Multiple linear regressions were used to evaluate the influence of biophysical site variables on conifer height at year 8 and height increment over the 7th and 8th growing seasons on site. Models were fit using the lm function in R Statistical Software v4.5.0 (R Core Team, 2021). Candidate biophysical site variables included basal area of surrounding trees, canopy openness, leaf area index, percent above-canopy light, relative water content, number of hardwood stumps within 2.5 m, understory vegetation cover, and fern cover. Interaction terms between planted tree species (redwood or Douglas-fir) and biophysical variables were initially included in the candidate models to test whether relationships differed between redwood and Douglas-fir. Model selection was based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). Models within $\Delta AIC \leq 6$ were considered candidate models, and AIC weights were calculated to help identify the "best" model. We selected best-fit models based on their parsimony and largest AIC weight.

Results

Redwood exhibited greater survival (93%) than Douglas-fir (67.5%) over 8 years since planting (Figure 1). Most of the mortality in Douglas-fir occurred between year 3 and 6 (84% of the total mortality recorded over 8 years). In total, 4.1% of planted redwoods and 2.4% of Douglas-fir sustained top damage. A subset of these damaged trees still alive in year eight (four redwood and three Douglas-fir) were excluded from the analyses of year-eight height and recent height increment (years 7 and 8).

Mean height at year eight was similar among species, and highly variable (Table 1). Maximum height for redwood was 45% greater than Douglas-fir. Average height increment over years seven and eight was 41% greater for redwood than Douglas-fir, with similar variation and comparable maximum increment. Relative to their average annual growth over 8 years on site, the height increment of redwoods was accelerating in years seven and eight (120% of redwood's 8-years average) while Douglas-fir height growth slowed (88% of Douglas-fir's 8-years average).

The best height model for planted conifers indicated that RWC and canopy openness were the strongest predictors of height after 8 years (Table 2). Species as a variable in the model was not significant, indicating that the analysis failed to detect differences in the year-8 height of redwood and Douglas-fir after taking into account the effects of canopy openness and soil moisture. Taller conifers had higher RWC and canopy openness for both species (Figure 2). Similarly, height increment over the most recent two growing seasons was also higher in locations with greater RWC and canopy openness (Table 2). Recent growth differed significantly between species, with redwood exhibiting more rapid height growth than Douglas-fir over the past 2 years across gradients of RWC and canopy openness (Figure 3). Plausible alternate regression models for year-8 height consistently showed that height was better predicted by canopy openness than the understory light variable, suggesting lesser importance of understory light than other factors such as below-ground competition. Plausible alternate models for height increment that included interaction terms indicated that impacts of soil moisture and canopy cover differed between planted redwood and Douglas-fir (Table 2).

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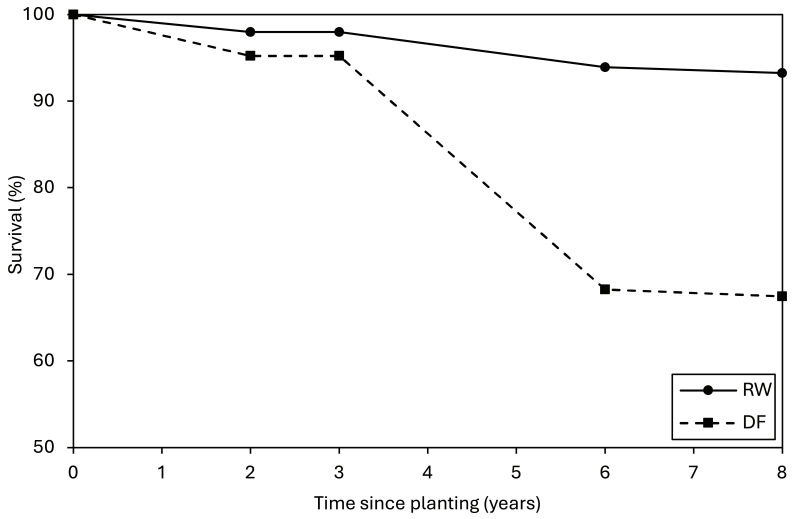


FIGURE 1
Survivorship of planted redwood (RW) and Douglas-fir (DF) over 8 years under a spatially-variable canopy outside redwood's range.

TABLE 1 Summary statistics for conifers planted under a spatially-variable canopy outside redwood's range: height after eight growing seasons and height increment over 7th and 8th growing seasons.

Variable	Species	*n*	Mean	s.d.	Min.	Max.
Tree height (cm)	Douglas-fir	72	171.0	74.1	54.9	399.3
	Redwood	122	176.9	105.3	29.0	579.1
Tree height increment (cm yr^{-1})	Douglas-fir	70	18.8	17.8	1.3	109.6
	Redwood	127	26.6	21.2	0.6	102.1

Discussion

Redwood exhibited higher survivorship over 8 years since planting, and more recently in year 7 and 8 it exhibited greater height growth than Douglas-fir, while average height remained similar between species. These findings from outside redwood's range are consistent with Schneider et al. (2023) who also found greater initial survival of redwood planted inside redwood's range than Douglas-fir under different levels and patterns of retention. Our VDR treatment generated substantial structural heterogeneity within the stand, reflected by the wide range in planted conifer height. Spatial heterogeneity in retention likely promoted variable access to light and soil moisture contributing to the large range in early growth of individual conifers. While mean height did not differ between species at year eight, current height increment for redwood exceeded that of Douglas-fir suggesting it may gain a height advantage as the stand develops. Our findings suggest that redwood can establish and perform competitively under warm and dry inland conditions when planted following VDR treatment, indicating potential for redwood planted beyond its typical coastal fog belt range (Dagley et al., 2017).

Planted Douglas-fir experienced elevated mortality, particularly between years three and six. Mortality appeared to be associated with higher overstory basal area in the immediate vicinity of each conifer, implying that local competition for soil moisture may have contributed to reduced survivorship more than other factors tested such as reduced understory light, itself a function of overstory tree density to the south of each planted conifer. The average basal area around planted Douglas-fir that subsequently died was significantly higher than the basal area around Douglas-fir that survived (32.1 and 22.5 m^2 ha^{-1}, respectively; p = 0.014). Average basal area for dead and surviving redwood was more similar at 28.2 and 21.8 m^2 ha^{-1}, respectively. These results indicate that Douglas-fir can establish and survive in multiaged stands, particularly in areas of lower overstory basal area with less moisture stress and shade, but growth is expected to slow over time under the expanding canopy (He and Duncan, 2000; Puettmann et al., 2021). This finding is consistent with literature synthesized by Hermann and Lavender (1990) where Douglas-fir seedlings can tolerate only light shade soon after establishment and become increasingly dependent on light as they age. In contrast, redwood is tolerant of shade, capable of surviving under more canopy cover than Douglas-fir, albeit with reduced growth (Olson et al., 1990).

Climatic conditions during the study period may have further exacerbated stress from shade and competition for limited growing space. The study area experienced drought over the first 2 years after planting, at which time planted conifers fared best in the gap treatment and redwood exhibited less evidence of drought stress than Douglas-fir (Kerhoulas et al., 2020). In 2020, annual precipitation was unusually low (979 mm; 26% below average) and coincided with an elevated vapor pressure deficit (VPD = 12.87 hPa) (PRISM Climate Group, 2020). By this time, the understory had become crowded with other vegetation, likely competing for limited soil moisture over the dry summer season. Douglas-fir growth has been shown to be constrained by limited summer moisture, especially with higher temperature years

TABLE 2 Plausible candidate models (within 6 AIC of best model) for height (H; cm) 8 years after planting, and height increment (ΔH; cm yr^{-1}) over 7th and 8th growing seasons as a function of canopy openness (CO; %), relative water content (RWC; %), and categorical species identity (Sp.; redwood = 1, Douglas-fir = 0).

Model	R^2	$R^2_{adj.}$	AIC	Δ AIC	Wt.
Total height 8 years after planting (n = 197)					
$\mathbf{H^{0.5} = 5.9985 + 0.0461RWC + 0.1294CO}$	**0.047**	**0.036**	**901.44**	–	**0.41**
$H^{0.5} = 0.0743RWC + 0.1890CO - 0.0010RWC*CO$	0.047	0.030	903.39	1.94	0.16
$H^{0.5} = 0.0446Sp + 0.0460RWC + 0.1300CO$	0.047	0.030	903.43	1.99	0.15
$H^{0.5} = -2.891Sp + 0.0460RWC + 0.0665CO + 0.0973Sp*CO$	0.050	0.027	904.89	3.45	0.07
$H^{0.5} = 0.0466Sp + 0.0743RWC + 0.1898CO - 0.0010RWC*CO$	0.047	0.024	905.38	3.94	0.06
$H^{0.5} = -0.0907Sp + 0.0448RWC + 0.1302CO + 0.0022Sp*RWC$	0.047	0.024	905.43	3.99	0.06
$H^{0.5} = 0.0446Sp + 0.0460RWC + 0.1300CO$	0.051	0.022	906.79	5.35	0.03
$H^{0.5} = -3.0351Sp + 0.0849RWC + 0.1455CO + 0.1022Sp*CO - 0.0013RWC*CO$	0.051	0.021	906.82	5.38	0.03
$H^{0.5} = -3.7763Sp + 0.0404RWC + 0.0613CO + 0.0097Sp*RWC + 0.1072Sp*CO$	0.047	0.021	907.38	5.94	0.02
Recent height increment (n = 194)					
$\mathbf{(\Delta H)^{0.5} = 1.2651 + 0.7140Sp + 0.0230RWC + 0.0480CO}$	**0.069**	**0.052**	**701.58**	–	**0.28**
$(\Delta H)^{0.5} = -0.3513Sp + 0.0122RWC + 0.0492CO + 0.0176Sp*RWC$	0.073	0.051	702.73	1.16	0.16
$(\Delta H)^{0.5} = 0.7114Sp - 0.0336RWC - 0.0690CO + 0.0019RWC*CO$	0.073	0.050	702.83	1.25	0.15
$(\Delta H)^{0.5} = 0.7079Sp + 0.0228RWC + 0.0479CO + 0.0002Sp*CO$	0.069	0.046	703.58	2.00	0.10
$(\Delta H)^{0.5} = -0.4769Sp - 0.0527RWC - 0.0826CO + 0.0196Sp*RWC + 0.0022RWC*CO$	0.078	0.050	703.79	2.21	0.09
$(\Delta H)^{0.5} = -0.9411Sp + 0.0116RWC + 0.0379CO + 0.0187Sp*RWC + 0.0172Sp*CO$	0.073	0.045	704.68	3.10	0.06
$(\Delta H)^{0.5} = 0.9105Sp - 0.0343RWC - 0.0659CO - 0.0066Sp*CO + 0.0019RWC*CO$	0.073	0.045	704.68	3.24	0.06
$(\Delta H)^{0.5} = 0.0246RWC + 0.0421CO$	0.037	0.025	705.29	3.72	0.04
$(\Delta H)^{0.5} = -0.8603Sp - 0.0522RWC - 0.0882CO + 0.0203Sp*RWC + 0.0112Sp*CO + 0.0021RWC*CO$	0.078	0.045	705.76	4.19	0.03
$(\Delta H)^{0.5} = -0.0334RWC - 0.0782CO + 0.0020RWC*CO$	0.041	0.024	706.52	4.95	0.02

Best models shown in bold. Wt. = AIC weight.

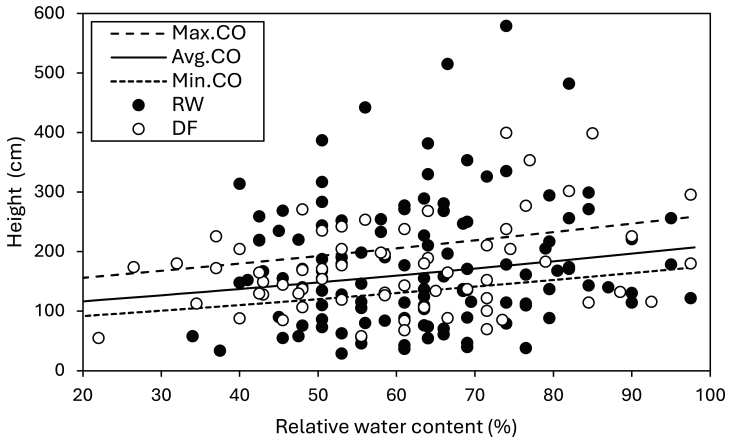


FIGURE 2
Relationship between height (cm) after eight growing seasons and relative water content (%). Points show observed values for individual redwood (RW) and Douglas-fir (DF) seedlings; lines represent the best-fit model prediction with maximum (43.07), average (29.94), and minimum (20.56) canopy openness (CO, %) held constant.

(Littell et al., 2008; Beedlow et al., 2013; Restaino et al., 2016), and that partial harvesting that reduces stand density promotes resistance to drought (Dagley et al., 2023).

Redwoods possess several biological traits that make this species suited for restoration in fire-prone landscapes of the western USA. Mature redwood trees have thick bark that protects the cambial layer from heat (Berrill et al., 2020). They also contain little to no flammable resin or pitch (Forest Products Laboratory, 2021). After harvesting or high-intensity fires that damage or kill redwood, it can resprout from stump and/or basal sprouts, allowing stands to recover rapidly after disturbance (Ramage et al., 2010; Muma et al., 2022; Kane and Carrasco, 2025).

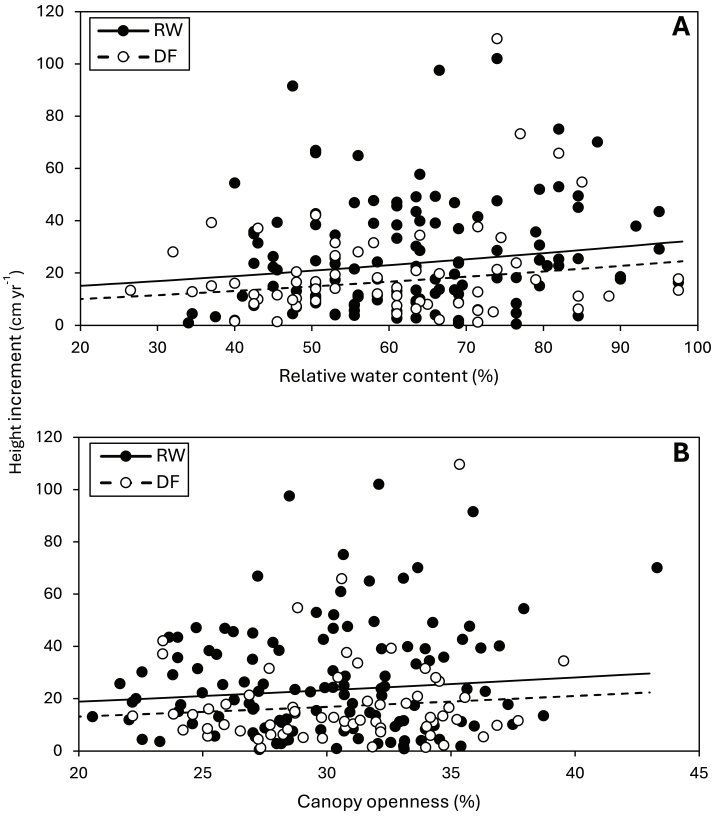


FIGURE 3
Relationship between height increment (cm yr^{-1}) over 7th and 8th growing seasons and **(A)** relative water content (%) or **(B)** canopy openness (%). Points show observed values and lines represent model predictions for planted redwood (RW) and Douglas-fir (DF).

There is a lack of published information describing early survival or height growth of planted redwood (Table 3). Most existing literature on early growth focuses on natural regeneration, particularly stump sprouting following harvest (Neal, 1967; O'Hara and Berrill, 2010; Muma et al., 2022), rather than nursery-grown planting stock. The few studies that do report growth of planted redwood are mostly from within the species' native range. Schneider et al. (2023) found that survival of planted redwood was influenced by canopy retention and local site conditions following selection harvesting, with the lowest survival occurring on southwest aspects and the highest survival under the light shade of a dispersed overstory. Even fewer studies have reported height and height increment for redwood planted across different sites and stand structures, limiting our ability to generalize about

TABLE 3 Comparing growth of planted redwood across California studies differing in stand structure (even-aged, EA vs. multiaged, MA), location, and age.

Measurement interval (yrs)	Age (yrs)	Periodic height increment (cm yr^{-1})	Average height increment (cm yr^{-1})	Location (Calif. County)	Stand structure	Within natural range (Y/N)	Study
11–13	13	44.3 (NA)	46.3	Humboldt	MA	Y	Berrill et al., 2021
6–13	13	26.5 (13.9)	26.9	Humboldt	EA	N	Murphy, 2025
6–13	13	52.3 (17.5)	49.6	Humboldt	EA	N*	Murphy, 2025
6–8	8	26.6 (21.2)	21.7	Humboldt	MA	N	Present study
4–5	5	11.1 (12.4)	11.7	Mendocino	MA	Y	Schneider et al., 2023
7–9	9	20.2 (NA)	22.7	Mendocino	EA	Y	Jameson and Robards, 2007

*Within redwood natural range, at eastern range margin, but no evidence of redwood occurring naturally at this location. Periodic height increment (cm yr^{-1}) represents mean annual height growth calculated over indicated measurement interval with standard deviation (in parentheses) when available. Average height increment (cm yr^{-1}) represents total height divided by age. Studies are ordered from north to south.

early performance of planted redwood, particularly in drier inland environments.

Our results indicate that height growth of redwoods planted after VDR harvest outside of redwood's range was similar to growth reported for redwood planted in some even-aged and multiaged stands (Table 3). Conversely, height growth reported for planted redwoods (age 13) in Berrill et al. (2021) and Murphy (2025) was nearly double the growth observed in our study. This discrepancy is likely related to differences in site quality, defined here primarily by soil moisture availability, canopy retention level, and competitive pressure from surrounding vegetation. This difference may also reflect the documented growth pattern where planted redwoods commonly exhibit slow initial growth while they become established, followed by rapid height increment from year ten onward (Olson et al., 1990). While the studies compared in Table 3 differ in stand age, structure, and site conditions, the general pattern of variation in growth among studies of early redwood height growth may be influenced more strongly by site-specific conditions than the stand's general geographic location in terms of latitude or distance from the Pacific Ocean.

Biophysical measurements were collected 5 years prior to the final growth measurements and analysis. These early measurements provide an understanding of baseline site conditions, however, canopy structure and competitive environments may have changed during the intervening period, particularly as overstory trees grew and their canopy began to close as the stand developed. As a result, biophysical variables used in this analysis should be interpreted as indicators of general site conditions rather than exact measurements of the growing conditions experienced by the trees over the full 8-year period. In addition, this study represents a single site located outside the coastal fog belt. Adding study sites across a broader geographic range would help strengthen the generality of these findings.

Continued monitoring will be important to assess whether these early patterns persist as the stand develops and how performance of planted conifers interacts with changing climate and increasing competition from overstory trees. Future work should explore how varying retention, light, soil moisture, and competing vegetation management interact to influence development of planted conifer nursery stock when utilizing VDR silviculture. Incorporating redwood into mixed-conifer plantings under VDR could support timber production objectives as well as restoration objectives by enhancing structural complexity (tree-size variability), species redundancy, and resistance to wildfire and climate change in these dry inland forests. Long-term resistance and resilience may also be enhanced once redwoods attain larger diameters and develop thick fire-resistant bark and/or resprout to rapidly reoccupy the site after future disturbances such as timber harvest or wildfire.

We expect that VDR silviculture could be used in many forest types, in any single-species or mixed stand with any tree species of mid- to high shade tolerance. More light-demanding species may only regenerate and grow well within gaps while more tolerant species have the potential to establish and perform well throughout the stand. There is also flexibility to tailor VDR prescriptions to meet local conditions and constraints. Specifically, the spatially-heterogeneous patterns of overstory tree retention can be varied in scale, intensity of variability, and species composition to meet restoration reference conditions or other landowner objectives. For example, changing the scale of the pattern of retention could be achieved by selecting a larger harvest patch size to reduce fine-scale spatial heterogeneity in the overstory which would reduce variability in growth in the new cohort, or vice versa. The intensity of spatial variability in overstory retention can be attenuated by avoiding creating gaps and/or uncut "skip" patches and instead just varying retention across a narrower range of retention levels, or by prescribing retention of one or more reserve trees within gaps instead of completely clearing gaps. Varying the species composition of retention among patches would further enhance variability, as would planting different combinations of species in each patch after harvest. Natural regeneration could also be supplemented by planting species native to the area that did not regenerate well and/or to enhance forest resilience via assisted migration by planting selected genotypes or species expected to be better adapted to future climates.

Data availability statement

The original contributions presented in this study are included in this article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

GL: Writing – original draft, Writing – review & editing, Conceptualization, Formal analysis. CD: Methodology, Supervision, Writing – review & editing. J-PB: Conceptualization, Methodology, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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