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Residual Stand Structure and Topography Predict Initial Survival and Animal Browsing of Redwood and Douglas-Fir Seedlings Planted in Coastal Forests of Northern California

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Abstract: Successful regeneration of commercial species is central to the long-term sustainability of forests managed for wood production. We studied two species of tree seedlings planted after group selection and single-tree selection harvesting in a 20 ha replicated silviculture experiment in stands dominated by coast redwood (*Sequoia sempervirens* (D.Don) Endl.). Treatments consisted of complete harvest in 1 ha group selection opening (GS), low-density dispersed retention (LD), aggregated high-density retention (HA), and dispersed high-density retention (HD). One year after planting, seedlings planted on a southwest aspect had the lowest survival rate, while northeast aspects had nearly complete survival rates. As expected, redwood had a higher survival rate than coast Douglas-fir (*Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco). Survival rates exhibited a rise-peak-fall pattern with stand density, most notably on southwest-facing slopes, ranking LD > HA ≈ HD > GS treatments. Deer browsing of planted seedlings was a pervasive problem where Douglas-fir were preferentially browsed over redwood. In treatments with higher retention densities, browsing was less likely, ranking GS > LD > HA > HD treatments. Further from watercourses at higher elevation, the probability of browsing diminished. Overall, dispersed treatments outperformed aggregated and GS treatments by simultaneously maximizing survival and minimizing browsing of planted seedlings. We did not perform site preparation or herbicide treatment of re-sprouting hardwoods following harvest, and therefore recommend testing the effectiveness of understory vegetation management to enhance seedling survival. Consideration could also be given to planting more seedlings in anticipation of lower survival rates, and/or implementing seedling protection measures when and where heavy browsing is expected.

Keywords: deer browsing; forest regeneration; plant–animal interactions; *Pseudotsuga menziesii*; *Sequoia sempervirens*; selection silviculture; sustainable forest management; tree planting

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1. Introduction

The regeneration of trees is critical to sustainable forest management, but seedling mortality can be a hindrance to successful regeneration in managed forests due to biotic and abiotic factors [1]. Climate, herbivory, and pathogens can affect the survival of seedlings in many forest types [2–4]. The interactions among herbivores, competing vegetation, topography, and type of silvicultural treatment are known to affect the survival, growth, and future form of planted tree seedlings [5–8]. For example, in silvicultural treatments of lower densities or within group selection openings, there is more competition from other vegetation while protection from climatic stress and predation is diminished [1]. The retention of intermediate density levels can enhance the early survival and growth of planted seedlings [9–11].

The rate of seedling and sapling height growth generally increases at a decreasing rate as more light becomes available [1,12,13]. Berrill et al. [14] reported slightly diminished growth of redwood and Douglas-fir seedlings planted adjacent to sprouting hardwood stumps. Redwood stump sprouts exhibit faster early growth than planted seedlings [15], so rather than planting seedlings near sprouting stumps, it is common practice to interplant between distant stumps where less competition is expected [16]. Little is known about how the growth and survival of planted redwood and Douglas-fir seedlings competing with natural regeneration differs under group selection or single-tree selection with either dispersed or aggregated patterns of retention. For other forest types, optimal survival and growth of planted seedlings typically occurs under a managed uneven-aged overstory where a compromise is reached between shelter, competition, and available resources such as understory light [17–22].

Seedling survival and growth can also be impacted by browsing. Over the past century, fire suppression and decreases in the size and number of timber sales on public lands and other contributing factors have created a decline in browsing habitats in northern coastal forests [23,24]. Because of this, black-tailed deer (*Odocoileus hemionus columbianus*) often rely on recently harvested stands for forage [25]. Browsing can have a direct effect on seedling survival rates and results in reduced seedling densities [26–28]. Seedling predation can also affect sustainable seedling growth and give a competitive advantage to less palatable tree and plant species [29–33]. New shoots are the most actively growing and nutritious parts of seedlings and are preferentially selected by deer [34,35]. Continued browsing of this terminal leader can reduce height growth and cause early mortality [36–40]. For Douglas-fir, redwood, and other conifer species, the first few years is when seedlings are most susceptible to wildlife damage, as they have not yet grown above browsing height. Herbivory of elk and deer in coastal forests is the most common and widespread form of damage to planted seedlings in the western US and Canada [41–43].

Little is known about relationships between the browsing of tree seedlings, topography, and disturbances from management activities. Deer can occupy coastal regions for the entire year, and the greatest impacts by deer herbivory take place in these coastal regions where deer can browse in any season [44–47]. It is also known that deer respond to changes in forest cover [11,48–50]. Examining the relationships between silviculture treatments and browsing of seedlings may allow us to determine which treatments reduce the incidence of browsing on planted seedlings, while enhancing their survival. Successful redwood natural regeneration resulting from seed is rare, and because of this, planting is often a more reliable approach to restoring conifer dominance in areas where conifers have not regenerated naturally [51,52].

We examined the effects of different selection silviculture treatments on the first-year survival of planted seedlings at four different sites in Mendocino County, California. We sought to answer the following questions:

(1) How does the spatial arrangement and density of the residual overstory affect the survival and herbivory of planted seedlings?
(2) How does the location of planted seedlings on the landscape (aspect, elevation, etc.) influence seedling survival and herbivory?
(3) Which treatment results in low browsing occurrence while also providing high seedling survival rates?

To our knowledge, this is the first study to examine survival and browsing of seedlings planted in mixed multiaged coast redwood stands.

2. Materials and Methods

2.1. Site Description

Jackson Demonstration State Forest (JDSF) is a 20,000 ha forest located on the northern coast of California, near the middle of redwood's natural range (39°21′ N 123°36′ W). Most of the old-growth redwood forests in this area were harvested in the 1900s and many of the resultant second-growth forests were subsequently harvested one or more times using single-tree selection, group selection, commercial thinning, or clearcutting. This resulted in a mix of multiaged stands and even-aged (second-growth and third-growth) stands. These disturbances released sprouting hardwoods, especially tanoak (*Notholithocarpus densiflorus* (Hook. and Arn.) Manos, Cannon and S.H.Oh), to occupy more growing space, and even dominate in some areas. Despite this, redwood is still dominant across the landscape, and commonly associates with Douglas-fir, tanoak, grand fir (*Abies grandis* (Douglas ex D. Don) Lindley), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Pacific madrone (*Arbutus menziesii* Pursh), giant chinquapin (*Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmq.), and red alder (*Alnus rubra* Bong.).

On JDSF, the soils are well-drained, loamy moderately deep to deep, and derived from sandstone. Topography varies from steep slopes to valleys with ephemeral or permanent streams. Valley bottoms consist of soils with low to moderate permeability which are gravelly and deep. Elevation varies from 20 m near the coast up to 700 m further inland near the crest of the Coast Range. Precipitation is relatively high in this temperate rainforest, ranging annually from 100 cm near the coast to 130 cm further inland and 90% of it occurring between the months of October and April. This Mediterranean climate is typified by cool, moist winters and hot, dry summers. Near the coast, the summer heat is moderated by coastal fog, which also adds additional moisture by deposition and comprises up to 45% of annual requirements for transpiration of coast redwood trees [53].

2.2. Experimental Design

We established a manipulative randomized-block experiment with four selection silviculture treatments replicated at four sites. Before partial harvesting to implement treatments, four square 2 ha experimental treatment blocks were laid out side-by-side, except at one site where a fifth block was included. Preharvest tree size ranged from 41 to 48 cm quadratic mean diameter and stand density ranged from 710 to 1640 stand density index (SDI). The treatments replicated at each site were complete harvest within a 1 ha group selection opening (GS), low-density dispersed retention (LD), and either aggregated (HA) or dispersed high-density retention (HD). Each treatment had a predefined density management zone (DMZ; [54]). The residual SDI of each treatment plot was calculated using the summation method suited to uneven-aged stands with non-normal diameter distributions [55], then divided by the maximum SDI for redwood (2470 [56]) to derive relative density. The goal for stand density after harvesting was 13% relative density post-harvest for the dispersed low-density treatment (LD), and 21% for both the aggregated and dispersed high-density treatments (HA and HD). The expectation was for stands to return to either 30% relative density for low-density or 50% for high-density treatments before the next harvest entry. Partial harvesting using cable yarder or ground-based systems began in autumn of 2011 and was completed by autumn of 2012. Aggregates or “clumps” were created by leaving three to four residual trees in a clump. Clumps consisted of redwood or a mixture of redwood, Douglas-fir, and sometimes tanoak. In dispersed treatments, aggregates of residual trees were avoided as much as possible to introduce a less “clumpy” structure that was more uniform in spatial pattern. We attempted to retain a species composition of 70–75% redwood, 20–25% Douglas-fir, and 0–5% tanoak consistently among treatments and across all four sites. Following partial harvest, advance regeneration and logging slash were lopped and scattered.

2.3. Data Collection and Analysis

After harvest, a single 0.2 ha (45 × 45 m) measurement plot was installed within each 2 ha treatment block. Trees within each plot were measured for diameter at breast height (DBH), height, and live crown base height. An intimate mixture of 25–30 redwood and 25–30 Douglas-fir seedlings were planted throughout each plot as far away as possible from residual trees and stumps of sprouting species. Seedlings were planted in the winter of 2012/2013 at two sites and the winter of 2013/2014 at the remaining two sites.

Seedling height was measured at the time of planting and again one year after planting (i.e., in the spring of 2014 or the spring of 2015) along with an assessment of animal browsing to the leader of each planted seedling. Locations of planted seedlings were recorded by first collecting distance and azimuth from the nearest plot corner then converting to latitude and longitude. ArcMap was used to derive variables from a 10-m DEM using the ArcMap interpolation toolset. Seedling-level variables were species (categorical variable: Douglas-fir or redwood), distance to road, distance to watercourse, and elevation. Plot-level variables were average flow accumulation, aspect, and slope. Aspect data were transformed to range continuously from 0 to 20, where 0 = northeast, 10 = southeast or northwest, and 20 = southwest-facing plots. Additional plot-level variables represented either treatment as a categorical variable or residual stand density in terms of SDI and understory light in terms of percent above-canopy light (PACL) from hemispherical image analysis described by Berrill et al. [57].

Logistic mixed-effects regression analysis was used to study two binary response variables, seedling survival (1,0) and seedling browsing (1,0) over the first year after planting. Candidate explanatory variables tested for inclusion in the final models were seedling-level variables and plot-level topographic variables plus one of three variables representing growing space in terms of either: treatment type, SDI, or PACL. Generalized linear mixed-effects logistic regression analysis was used when the categorical treatment variable replaced continuous variables SDI or PACL in the analysis. Site was specified as a random effect. To determine the best combination of variables within a model, the Step AIC method of model selection was used. Models were then compared using Brier score, AIC and AICc values [58–60]. Data were analyzed using R version 3.2.3 (R Core Team, Vienna, Austria, 2015). Regression models were fit by maximum likelihood using the 'glmer' function in R package 'lme4'. Post hoc pairwise tests using 'emmeans' tested for differences among individual silvicultural treatments.

3. Results

3.1. Survival of Planted Seedlings

The data collected for seedling survival shows that there was a difference in survival (%) among sites and treatments (Figure 1 & Table 1). Underplanting of seedlings in the three single-tree selection treatments (i.e., HA, HD, LD) resulted in significantly higher survival rates than planting in GS openings ($p = 0.0028$ (HA); $p = 0.0001$ (HD); $p < 0.0001$ (LD)). Redwood seedlings had similar survival rates to Douglas-fir at north-facing sites (Figure 1). Generally, at the south and west-facing sites (Waldo North and Camp Six) there was a lower survival rate than at the north-facing sites (Waldo South and Whiskey Springs). The lowest survival rate for redwood was at Waldo North, which had aspects facing almost directly southwest. The Camp Six replicate occupied an exposed ridgetop and had the lowest survival rates for Douglas-fir.

Table 1. Summary data for residual stand (n = 17 plots) and seedlings planted in each treatment: group selection (GS), low-density dispersed (LD), high-density aggregated (HA), and high-density dispersed (HD). Browsing and survival percentage calculated for every plot and 'Mean' is average of those plots (n) on JDSF in Mendocino County, California, USA.

	Treatment	n	Mean	s.d.	Min.	Max.
Residual tree DBH (cm)	All	17	44.9	8.6	31.9	60.1
Residual tree density (stems ha^{-1})	GS	4	0.0	0.0	0.0	0.0
	LD	4	146.5	45.6	69.0	182.0
	HA	4	208.3	25.6	172.0	237.0
	HD	5	174.6	40.6	123.0	217.0

Table 1. *Cont.*

	Treatment	n	Mean	s.d.	Min.	Max.
Stand density index (metric)	GS	4	0.0	0.0	0.0	0.0
	LD	4	332.8	23.9	306.0	363.0
	HA	4	559.8	26.5	538.0	605.0
	HD	5	542.4	20.7	523.0	580.0
Planted density (seedlings ha^{-1})	All	17	271.1	29.2	232.1	325.9
Elevation of seedling (m)	All	934	236.2	39.4	176.0	326.0
Distance from watercourse (m)	All	934	218.5	70.8	78.0	354.0
Redwood seedlings						
Planted height (cm)	All	467	21.0	5.1	9.0	49.0
Height after 1 year (cm)	All	427	23.9	6.3	4.0	49.0
Not browsed (cm)	All	383	24.2	6.1	7.0	49.0
Browsed (cm)	All	44	22.0	7.7	4.0	40.0
Browsed (%)	GS	4	25.9	17.7	4.3	53.6
	LD	4	6.9	4.0	0.0	10.0
	HA	4	8.5	3.0	5.6	13.3
	HD	5	3.7	4.2	0.0	10.3
Survival (%)	GS	4	78.7	19.3	48.0	96.7
	LD	4	96.0	6.9	84.0	100.0
	HA	4	93.6	9.0	78.3	100.0
	HD	5	97.7	1.5	96.0	100.0
Douglas-fir seedlings						
Planted height (cm)	All	467	45.0	24.1	15.0	104.0
Height after 1 year (cm)	All	383	42.4	23.9	8.0	103.0
Not browsed (cm)	All	208	40.7	23.0	8.0	103.0
Browsed (cm)	All	175	44.4	24.8	13.0	93.5
Browsed (%)	GS	4	65.4	7.3	54.5	75.0
	LD	4	60.9	7.0	52.0	69.6
	HA	4	42.5	11.2	24.1	52.9
	HD	5	24.7	16.6	3.4	50.0
Survival (%)	GS	4	68.7	26.7	36.7	96.7
	LD	4	94.2	4.5	88.2	100.0
	HA	4	82.2	17.3	57.1	100.0
	HD	5	82.5	17.3	57.1	100.0

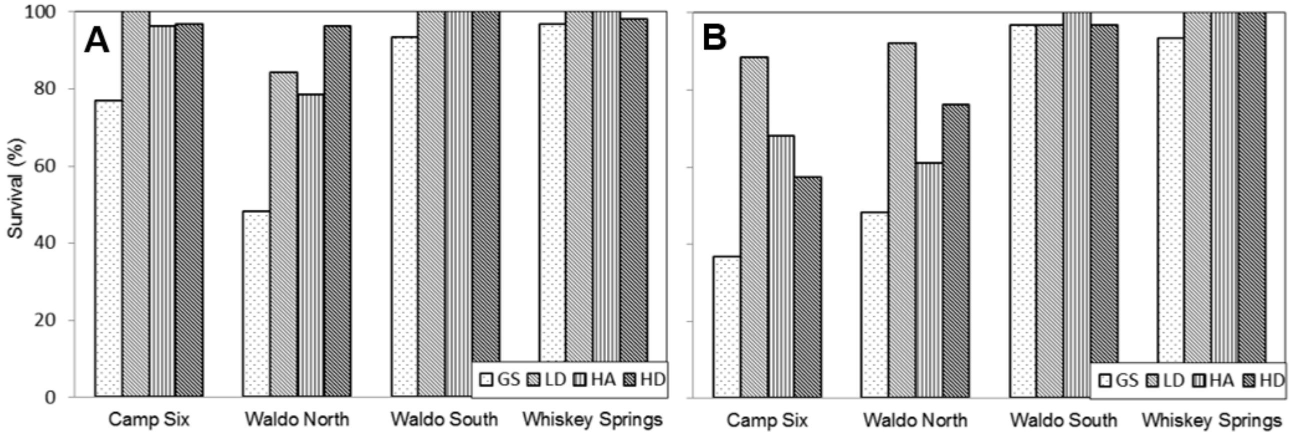


Figure 1. Seedling survival for redwood (**A**, n = 467) and Douglas-fir (**B**, n = 467) over first year since planting on JDSF in Mendocino County, California, USA.

The simpler "treatment model" had the same Brier score as the better fitting "aspect model" (Table 2), which suggested the predictive power was similar to the AIC-derived treatment model. The aspect model predicted that redwood seedlings had higher survival rates than Douglas-fir seedlings, except on northeast-facing slopes where both species had high survival rates (Figure 2). Pairwise tests indicated that survival was significantly lower in the GS treatment than other treatments ($p < 0.01$), but did not differ for Douglas-fir or redwood seedlings between HD and HA ($p = 0.99$), between HA and LD ($p = 0.06$), or between HD and LD ($p = 0.20$).

Table 2. Survival treatment-effect model coefficients (s.e. as percent of coefficient in parentheses) for redwood (n = 467) and Douglas-fir (n = 467) seedlings. Response = Survival probability (0–1).

	Aspect Model	**Treatment Model**
Modeling Method	GLMM	GLMM
Selection Method	AICc	AICc
Intercept	3.4744 (13%)	1.0781 (76%)
Treatment (LD)	2.3663 (16%)	2.3417 (16%)
Treatment (HA)	1.1822 (26%)	1.2486 (24%)
Treatment (HD)	1.3654 (22%)	1.4063 (21%)
Species (Redwood)	1.1187 (22%)	1.1221 (22%)
ln(Asp_trans+1)	−1.3693 (12%)	
Brier Score (MSE)	0.082	0.082
AICc	506.81	519.09
AIC	506.70	519.00
Log Likelihood	−250.10	−253.50

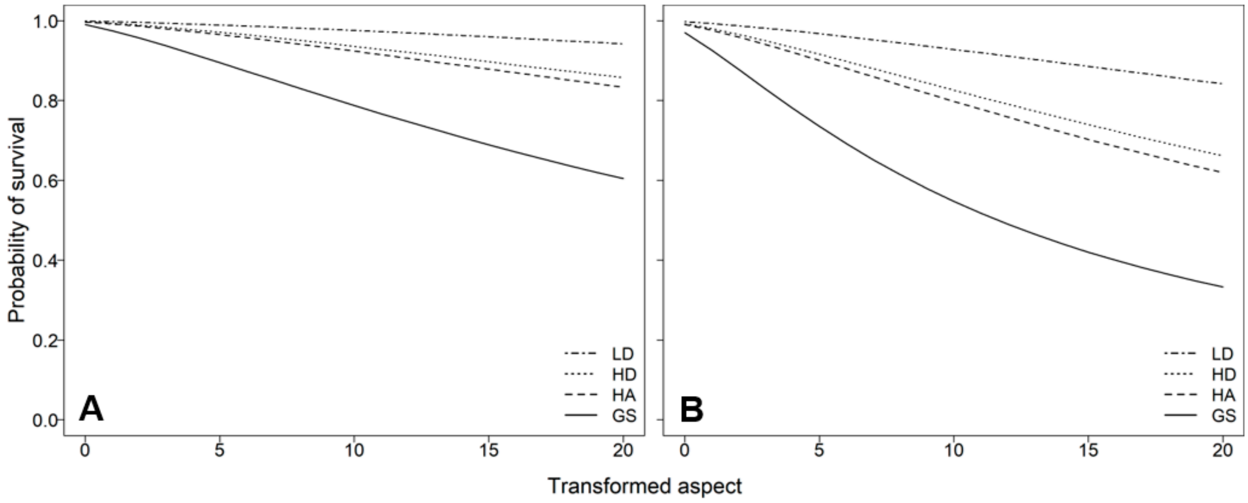


Figure 2. Predicted survival probability for redwood (**A**) and Douglas-fir (**B**) seedlings at transformed aspects ranging from 0 = northeast, 10 = northwest or southeast, and 20 = southwest.

Another set of models were created substituting SDI for treatment, which all had slightly poorer fit than the treatment models, except for the quadratic "SDI aspect model", which was the best fitting survival model (Table 3). This model included seedling species, SDI, and aspect as explanatory variables, and predicted a "rise-peak-fall" relationship between SDI and survival probability, indicating that the highest rates of survival were at densities of 100–300 SDI for both species (Figure 3A,B). When aspect was held constant at 0 (northeast aspect), the model predicted very close to 100% survival for both species regardless of SDI. As aspect approached the southwest (transformed aspect of 20), the probability of survival decreased substantially. This effect was more pronounced at lower residual stand densities (approaching 0), where survival was as low as 40% for Douglas-fir seedlings and 60% for redwood seedlings (Figure 3A,B). When SDI was held constant at 0, 300, and 600, the model predicted survival declining for both species at lower densities and on more southern or west-facing slopes (Figure 3C,D).

Table 3. Survival SDI model coefficients (s.e. as percent of coefficient in parentheses) for redwood (n = 467) and Douglas-fir (n = 467) seedlings. Response = Survival probability (0–1).

	SDI Aspect Model	**SDI Model**	**PACL Model**
Modeling Method	GLMM	GLMM	GLMM
Selection Method	AICc	AICc	AICc
Intercept	3.42765 (43%)	1.34830 (58%)	4.71737 (19%)
Species (Redwood)	1.12387 (24%)	1.04710 (22%)	1.04647 (22%)
SDI	−0.01467 (0%)	0.00247 (19%)	
$SDI^{0.5}$	0.40159 (8%)		
ln(Asp_trans+1)	−1.35206 (165%)		
PACL			−0.03537 (19%)
Brier Score (MSE)	0.080	0.088	0.089
AICc	502.12	543.48	544.42
AIC	502.00	543.40	544.00
Log Likelihood	−245.00	−267.70	−268.00

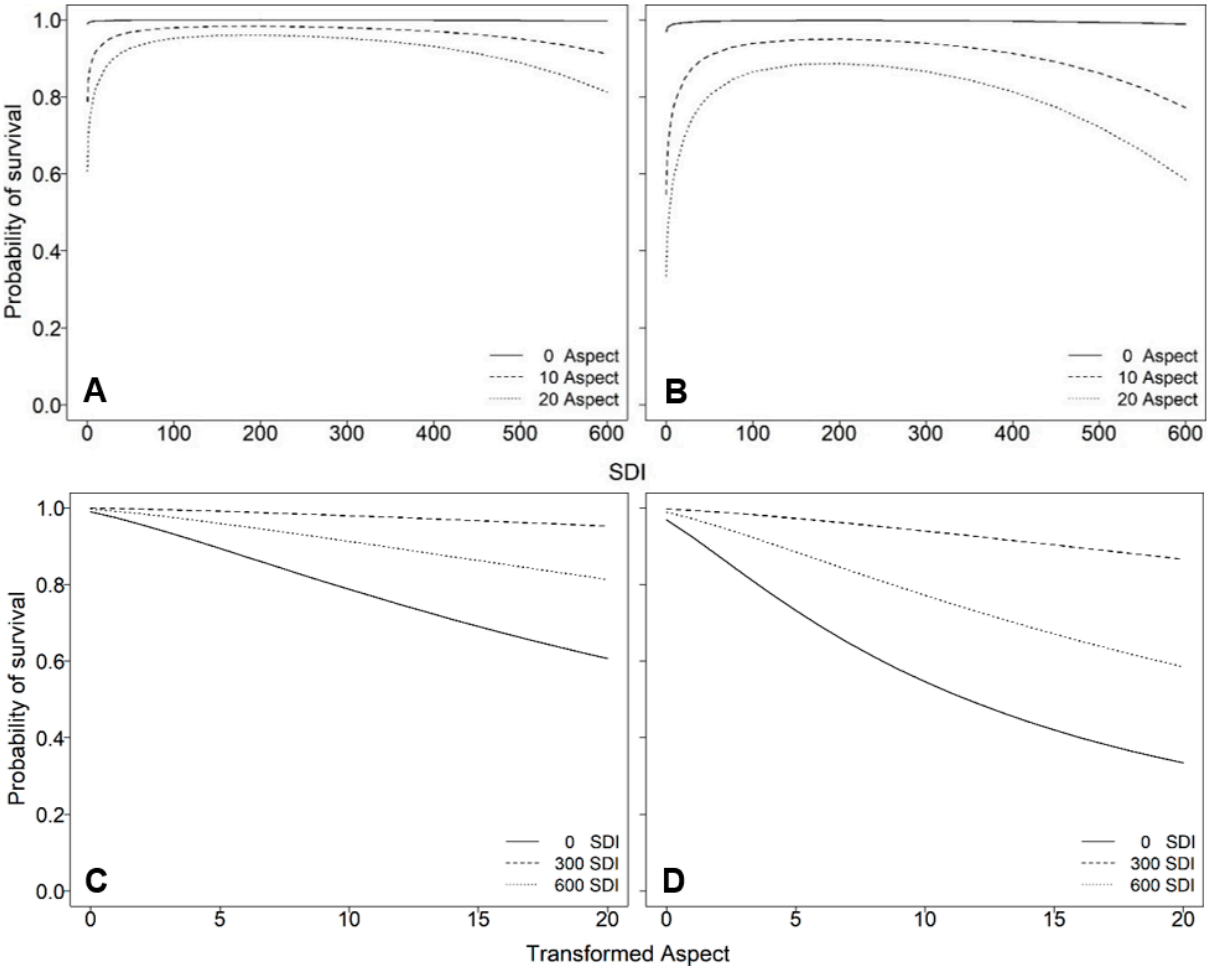
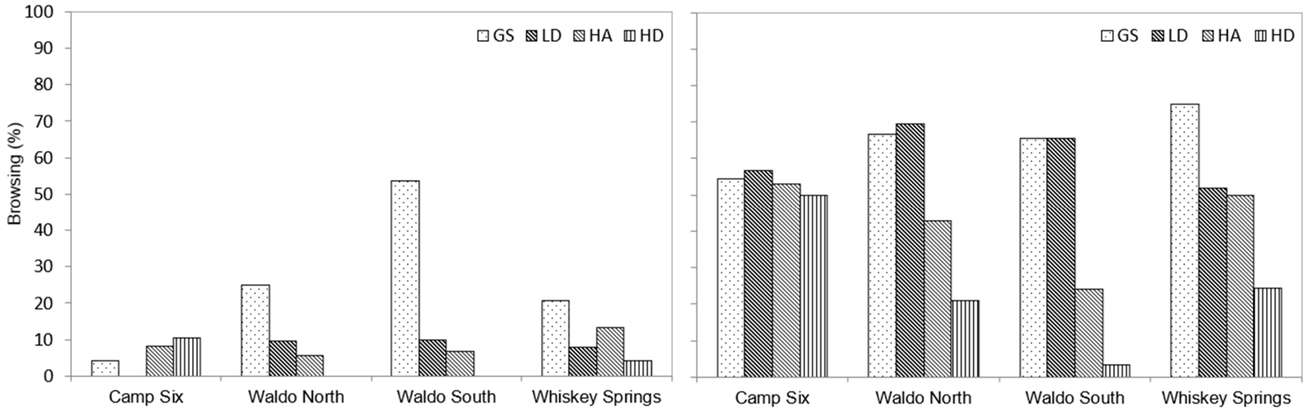


Figure 3. Predicted probability of survival for redwood (**A**,**C**) and Douglas-fir (**B**,**D**) when transformed aspect is held constant at three levels: 0 = northeast; 10 = northwest/southeast; 20 = southwest (**A**,**B**), and when SDI is held constant at three levels (**C**,**D**). Model formula is *survival* probability = $1/(1 + EXP(-1 \times ($ 3.42765 – (0.014673 × SDI) + (0.40158 × $SDI^{0.5}$) + 1.12387 (Redwood) – (1.352062 × (*ln*(Asp_trans+1)))).

Predicted survival was the highest for both species when SDI was at 300, and when seedlings were planted on northeast slopes (transformed aspect of 0). Redwood seedlings were predicted to have 60% survival at 0 SDI and 80% survival when SDI was 600 on southwest aspects. Douglas-fir seedlings were predicted to have less than 40% survival at 0 SDI and 60% survival when SDI was 600 on southwest aspects. PACL was tested as a predictor of survival probability but was not found to improve the model fit.

3.2. Browsing of Planted Seedlings

Browsing was found to be most common in the GS and LD treatments. There was a difference in browsing occurrence among treatments and sites, but more notably, there was much more browsing of Douglas-fir than redwood (Figure 4 and Table 1).



(**A**) (**B**)

Figure 4. Browsing percentage for redwood (**A**, n = 467) and Douglas-fir (**B**, n = 467) seedlings over first year since planting.

Redwood seedlings had a higher rate of browsing in the GS treatments than in any other treatment, except at Camp Six. The HD treatments appeared to minimize browsing occurrence in both species, while in the HA treatments on every site except Camp Six, browsing was nearly double what it was in the dispersed treatment of the same density (HD). This result suggested that browsing rates were affected by the spatial pattern of the overstory.

Browsing models were created using elevation, species, treatment type, and distance to watercourse. Distance to watercourse and elevation could not be included in the same model because they were correlated. The best browsing model used elevation, treatment type, and species as predictor variables (Table 4). Species was the most significant variable, indicating a greater probability of browsing in Douglas-fir ($p < 0.0001$). Elevation was also highly significant, indicating a greater probability of browsing at lower elevations ($p < 0.0001$). Pairwise tests indicated that browsing was significantly higher in the GS treatment than HD and HA treatments ($p < 0.02$) but not LD ($p = 85$); browsing was more likely in HA than HD treatments ($p = 0.03$), and between LD and HD ($p < 0.01$), but not between HA and LD ($p = 0.47$). The browsing probability of redwood was predicted to decrease to nearly 0% for all treatments at the highest elevations sampled. Browsing probability also decreased significantly for Douglas-fir as elevation increased, decreasing to 20% in the GS treatments at the highest elevations (Figure 5).

Table 4. Browsing treatment-effect model coefficients (s.e. as percent of coefficient in parentheses) for redwood (n = 467) and Douglas-fir (n = 467) seedlings. Response = Browsing Probability (0–1).

	Watercourse Model	Elevation Model	Treatment Model
Modeling Method	GLMM	GLMM	GLMM
Selection Method	AICc	AICc	AICc
Intercept	1.53878 (20%)	7.1962 (21%)	0.9433 (22%)
Treatment (LD)	−0.20480 (33%)	−0.8682 (29%)	−0.8733 (28%)
Treatment (HA)	−1.18367 (22%)	−1.4034 (19%)	−1.2606 (21%)
Treatment (HD)	−2.05548 (13%)	−2.2581 (13%)	−2.1691 (13%)
Species (Redwood)	−2.14636 (9%)	−2.1952 (9%)	−2.1359 (9%)
Elevation		−0.0264 (23%)	
Dist_stream$^{0.5}$	−0.00321 (38%)		
Brier Score (MSE)	0.152	0.149	0.153
AICc	763.01	753.44	767.81
AIC	762.90	753.30	767.70
Log Likelihood	−374.40	−369.70	−377.90

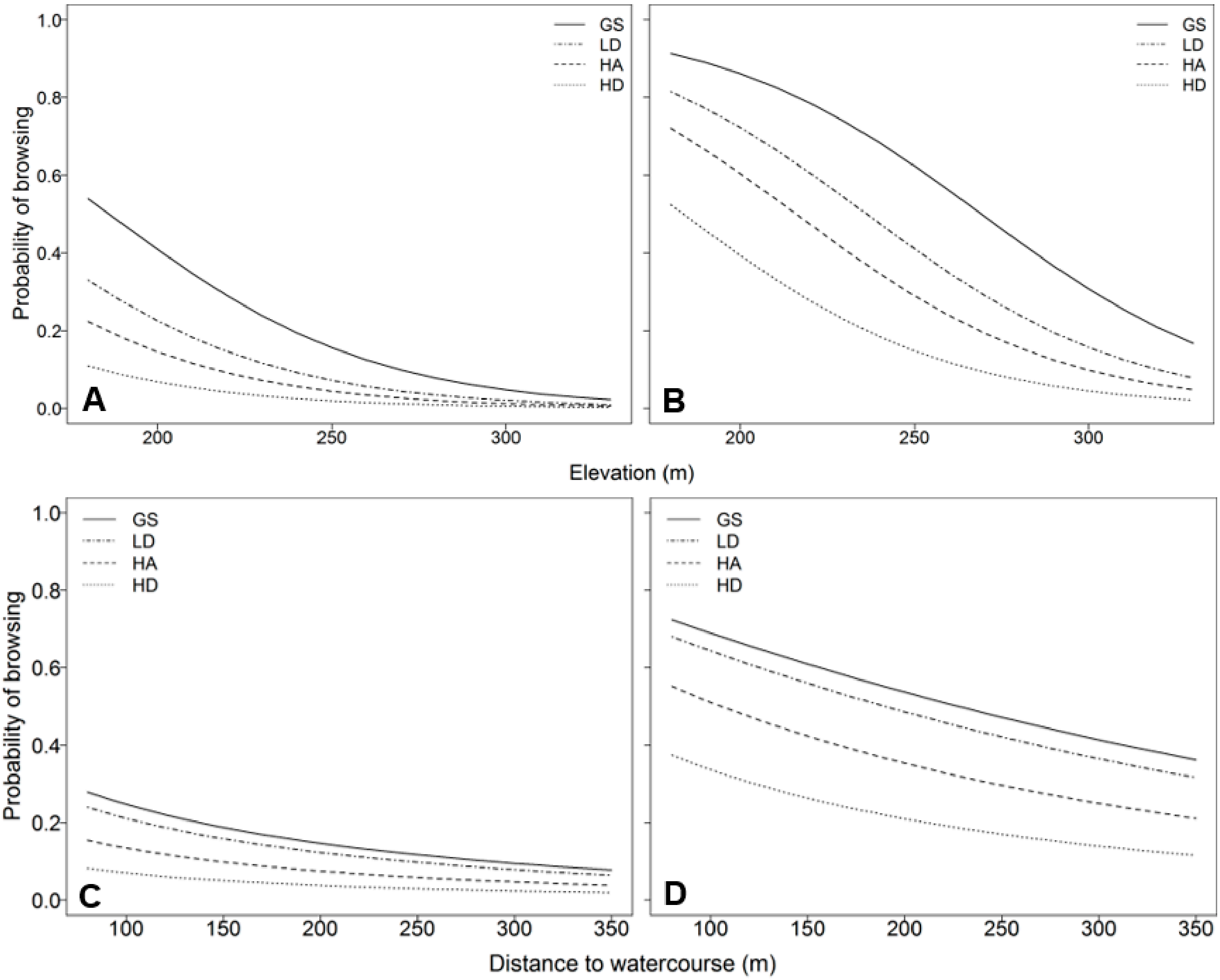


Figure 5. Predicted probability of browsing across a range of elevations and distances from a watercourse for redwood (**A**,**C**) and Douglas-fir (**B**,**D**) seedlings.

As the distance from a watercourse increased, the probability of browsing decreased (Figure 5). This effect was the same for both species and all treatments. Like the other treatment models, browsing was predicted to be most common in GS openings, followed by LD, HA, and HD treatments. The difference between HD and HA treatments was pronounced for Douglas-fir which experienced higher seedling browsing in aggregated retention treatments than dispersed retention treatments of the same density.

Like the survival models, browsing models were also fitted using SDI instead of treatment as a predictor variable to create models with flexible applicability. The elevation model was the best model using SDI. Although AICc was eight points higher than the treatment elevation model, the Brier score was similar, indicating it had similar predictive power (Tables 4 and 5). When SDI was held constant at three levels (0, 300, and 600), browsing was predicted to decrease as elevation increased, and was more likely at lower densities (Figure 6A,B). When elevation was held constant at three levels (180, 250, and 320 m), browsing decreased as SDI increased.

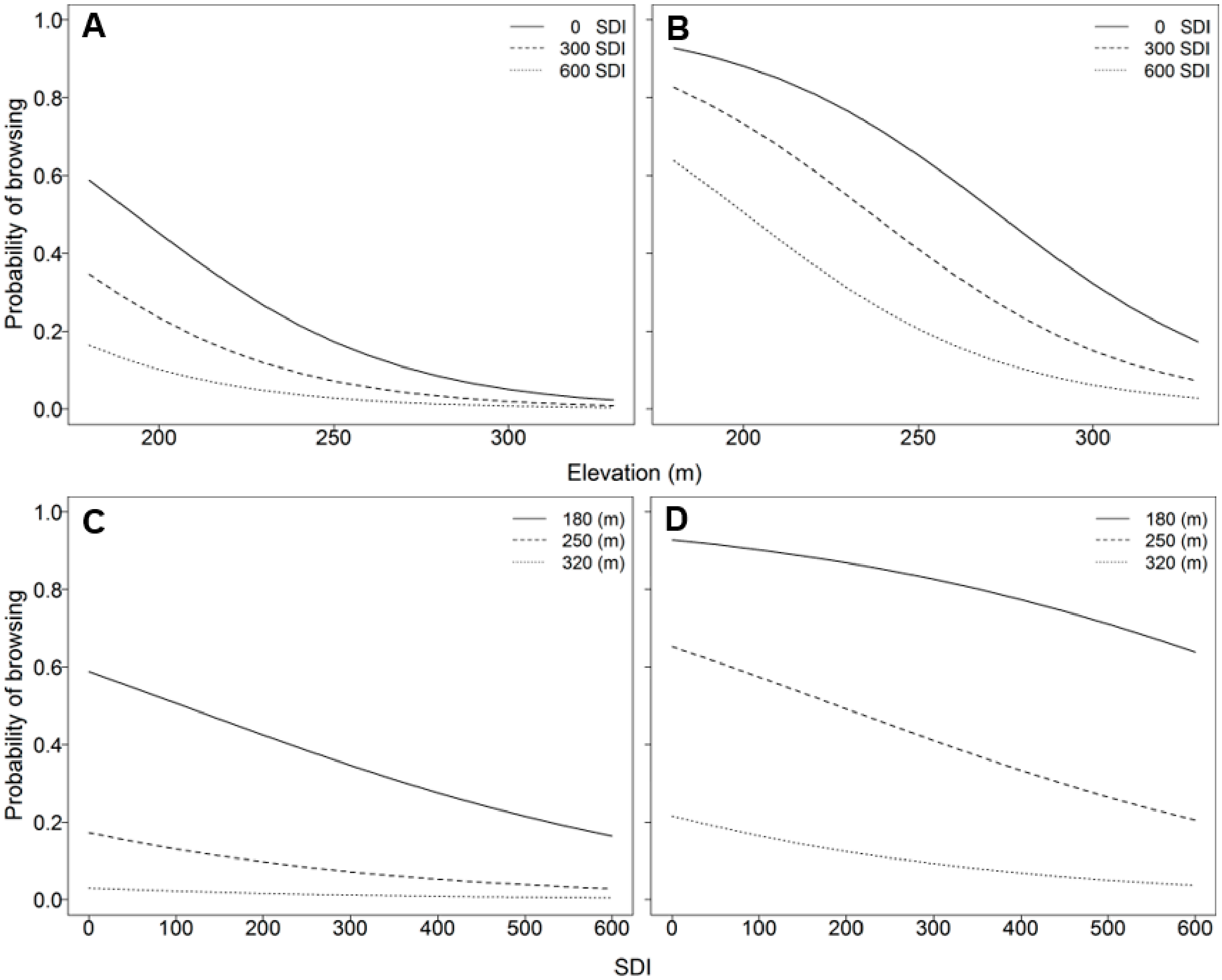


Figure 6. Predicted probability of browsing across a range of elevations when SDI is held constant at three levels, and across a range of SDI with elevation held constant at three levels, for redwood (**A**,**C**) and Douglas-fir (**B**,**D**) seedlings.

Table 5. Browsing SDI-effect model coefficients (s.e. as percent of coefficient in parentheses) for redwood (n = 467) and Douglas-fir (n = 467) seedlings. Response = Browsing Probability (0–1).

	Watercourse Model	Elevation Model	SDI Model
Modeling method	GLMM	GLMM	GLMM
Selection method	AICc	AICc	AICc
Intercept	2.80718 (24%)	7.03573 (20%)	0.96135 (20%)

Table 5. *Cont.*

	Watercourse Model	Elevation Model	SDI Model
Species (Redwood)	−2.16879 (9%)	−1.95506 (9%)	−2.11262 (9%)
SDI	−0.00262 (17%)	−0.00253 (13%)	−0.00306 (14%)
Elevation		−0.02838 (18%)	
Dist_sream$^{0.5}$	−0.00896 (31%)		
Brier Score (MSE)	0.154	0.150	0.155
AICc	769.70	761.50	778.21
AIC	769.76	761.40	778.20
Log Likelihood	−379.80	−375.70	−385.10

At a lower elevation of 180 m, the probability of browsing for redwood seedlings was the highest, and decreased from 60% at low densities (0 SDI) to 20% at high densities (600 SDI). For Douglas-fir seedlings, browsing probability remained relatively high (70%) as SDI approached 600 at the same elevation (180 m) (Figure 6C,D). The watercourse models predicting browsing probability dependent on treatment or SDI and distance to watercourse had lower goodness-of-fit but predicted the same trends and have more general applicability than elevation models limited to a specific elevation range (Tables 4 and 5). PACL was tested as a predictor of browsing probability but was not found to improve model fit.

4. Discussion

The sustainability of forests managed for timber production often hinges on the survival of planted seedlings. Aspect and treatment type were found to be the most influential variables for predicting seedling survival. Aspect and shade are known to affect the survival of planted seedlings [22,61–66]. Seedlings planted on a southwest aspect were predicted to have the lowest survival rates, while seedlings planted on northeast aspects were predicted to have nearly complete survival. This is consistent with Yu et al. [66] who studied several species of a pine-oak mixed forest in the mountains of China, and Germino et al. [64] who studied Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in Wyoming. Exposed sites with direct solar radiation can be stressful environments for planted seedlings. By planting seedlings in the shade, they can benefit from reduced evapotranspiration and foliar damage [67–69]. Redwood and Douglas-fir mortality rates were especially high in treatments where there was nearly full sunlight, suggesting that desiccation of these seedlings may have resulted in mortality. Survival model predictions indicated that GS treatments had the lowest survival rates for both species, while LD treatments had the highest rate of survival. Therefore, light shading of seedlings appeared to produce the most desirable results. This is consistent with a known characteristic of first year Douglas-fir seedlings, which survive best under light shade on south-facing slopes [70]. Our findings are also consistent with another shade-tolerant conifer, northern white-cedar (*Thuja occidentalis* L.), which exhibited higher survival in moderately open canopy conditions [71]. Our Douglas-fir seedlings had lower survival rates than redwood seedlings within the first year after planting, which might be explained by regional drought, deer browsing, planting effects, or the genetics of the planting stock [72].

In many forests, grasses and shrubs quickly invade after a disturbance [73–76], and these plants may interfere with a seedling's ability to survive. Even in multiaged stands, control of competing vegetation may be needed to ensure the establishment and survival of first-year seedlings as they may not grow quickly enough to outcompete the surrounding vegetation. In this study, shrubs and weeds were not controlled after partial harvesting, which may have impacted survival rates. Ward et al. [76] found that removing competing vegetation improved survival rates of seedlings, and Walters et al. [21] found that when not using weed control or deer fencing, single-tree selection treatments had higher seedling survival than other treatment types. This was similar to our findings: the treatments which had the highest survival probability were dispersed single-tree selection treatments.

Deer browsing of planted seedlings was a pervasive problem near watercourses, at lower elevations, and among vigorous seedlings planted in high light environments. This is consistent with Campbell et al. [77] who found browsing of several tree and shrub species in West Virginia was best predicted using elevation, and Walters et al. [21] who found browsing of 18 northern hardwood species in Michigan was more common in high light environments where competing vegetation was not removed.

Black-tailed deer are known to migrate seasonally to winter ranges at lower elevations and summer ranges at higher elevations, while some can maintain year-round range at middle to lower elevations [78–80]. This is similar to the observed behavior of mule deer (*Odocoileus hemionus* Rafinesque) in southern California [81] and sika deer (*Cervus nippon* Temminck) in Japan [82]. Black-tailed deer are also known to use watercourses for their migration routes. Consequently, it follows that deer would be more likely to browse seedlings at lower elevations and closer to streams. These habits of black-tailed deer were consistent with what was found in our study: there was a higher probability of browsing at lower elevations and closer to watercourses for both redwood and Douglas-fir seedlings.

Douglas-fir seedlings were preferred by browsing animals over redwood seedlings in this study. This was expected, as it is known that Douglas-fir is preferred winter and spring forage for black-tailed deer [83,84]. Redwood contains high levels of tannin, an allelochemical which interferes with the digestion of deer. This makes redwood less desirable for foraging [85]. Avoidance, or reduced preference for tannins during ungulate browsing has been observed in other research studies with other plant species [86–88].

Differences in browsing occurrence were evident among treatments, and GS treatments had the highest rates of browsing in this study. GS cuts and aggregated treatments increase the ratio of forest edge to forest area. Locations with an increased edge-to-area ratio are favored habitat for deer and can have increased occurrences of deer herbivory [37,89,90]. In future studies, it would be beneficial to have dispersed and aggregated treatments at multiple levels of density with different sizes of aggregates and gaps.

Unfortunately, instances of animal browsing were recorded for many of the planted seedlings which negated most/all height growth. The browsing damage may have masked or interacted with another potential impact on the growth of planted seedlings: belowground competition from established root systems of residual trees and sprouting conifer and hardwood stumps [91]. Trenching would be an effective approach to isolate the effects of above and below ground competition in these multiaged stands [92,93]. Browsing may have contributed to the mortality of seedlings, as has been noted in northern white-cedar [71]. Young seedlings may be vulnerable to browsing-induced mortality, but after a certain age they are more able to withstand the damage from repeated browsing [37]. Some deer repellents have shown efficacy in reducing browsing occurrence on conifer seedlings, but these preventative measures can be costly and time intensive to implement [94]. Deer fencing is an effective method for improving seedling survival, growth, and density by reducing the likelihood of browsing occurrence [76]. For example, [95] found that English oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) seedlings at low elevation sites in southern Sweden had 25% to 50% higher survival rates in fenced areas than in unfenced areas, and survival rates increased as canopy openness increased. Conversely, they observed that unfenced areas had lower seedling survival rates and increased browsing occurrence as canopy openness increased in these unfenced areas. This suggests that protecting a subset of seedlings from browsing, especially in group selection openings where more light is available, with fencing, shelters, or animal repellant to separate this impact on growth from other factors should be considered in future studies.

This seedling study coincided with a regional drought (2014–2015 [96]). The drought may have contributed to the desiccation and lower survival rates of planted seedlings, as well as greater competition for soil moisture resulting in reduced aboveground and belowground growth. We did not have enough replication across different years to test for climate × treatment interactions. In future studies, it may be useful to stagger planting across more than two years, and to consider watering a subset of seedlings to control for the effects of drought stress on planted seedlings within the first year of planting. Measurements of microclimatic factors such as soil moisture, relative humidity, and soil temperature should also be considered.

Our research informs managers of forests in north coastal California interested in underplanting after partial harvesting in coast redwood stands. Another application of this research is the restoration of conifer dominance through hardwood control and conifer underplanting [97]. On northeast-facing slopes, managers can expect seedlings of both species to have high survival rates regardless of treatment and residual stand density. On south-facing slopes, planting more seedlings to offset losses due to low survival may be the simplest mitigation approach, especially when harvesting using GS treatments. Removing competing vegetation to minimize competition, especially in GS treatments on south-facing slopes, could be another viable option. We did not test this but expect that weed control in the immediate vicinity of planted seedlings would help enhance survival of seedlings planted in hot, dry, high-light environments [21].

If the primary objective is the survival of planted seedlings, a dispersed treatment with low residual stand density will provide the best results according to our models. This range of retention levels equates to 10–30% relative density for pure redwood stands, or 12.5–37.5% relative density for a 50:50 redwood/Douglas-fir mixture. However, it should also be considered that ideal conditions for survival are unlikely to also provide ideal and sustainable conditions for seedling growth. Successful regeneration is a necessary crucial step to replace harvested trees, and to ensure the long-term sustainability of forest management for timber production. When the objective is to improve survival and reduce browsing impacts on planted seedlings in areas or treatment types where browsing is more likely (i.e., LD and GS treatments), the survival and browsing models in this study can aid managers in determining how many and where additional seedlings need to be planted and/or where seedling protection measures should be implemented to successfully regenerate an understory of redwood and Douglas-fir after partial harvesting in coast redwood stands.

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