NRC Research Press
ARTICLE

Effects on understory biomass and forage 8–10 years after precommercial thinning of Sitka spruce – western hemlock stands in southeast Alaska

Justin S. Crotteau, Annelise Z. Rue-Johns, and Jeffrey C. Barnard

Abstract: In southeast Alaska, United States, multiple-use forest management objectives include both timber production and wildlife habitat. Following stand-replacing disturbances such as clear-cutting, Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) naturally regenerate and competitively dominate resources, excluding understory biomass and biodiversity. Thinning may mitigate the effects of canopy closure and permit understory development, but evidence of the effect on understories 8–10 years after thinning is lacking. We report results 4–5 and 8–10 years after thinning experiments on the Tongass National Forest to demonstrate the effects of precommercial thinning (thinned versus control), stand age (15–25, 25–35, and 35–50 years), and weather on understory dynamics and Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam, 1898) forage availability. Stand density negatively affected understory biomass, whereas temperature and precipitation positively interacted to increase biomass. Thinning had an enduring effect on understories, with biomass at least twice as great in thinned versus unthinned stands through year 10. We identified compositional differences from thinning as stand age class increased. Deer forage responded similarly to biomass, but thinning-induced differences faded with increased winter snowfall scenarios, especially in older stands. This study aids the understanding of stand overstory and understory development following silvicultural treatments in the coastal temperate rain forest of Alaska and suggests management implications and applications for balancing objectives throughout the forest type.

Key words: Tongass-Wide Young-Growth Studies, Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), FRESH-deer model, understory diversity.

Résumé : Dans le sud-est de l'Alaska, aux États-Unis, les objectifs de l'aménagement forestier polyvalent incluent à la fois la production de matière ligneuse et l'habitat faunique. À la suite d'une perturbation majeure, telle la coupe rase, l'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière) et la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) se régénèrent naturellement et dominent les ressources de façon compétitive, excluant la biodiversité et la biomasse du sous-bois. L'éclaircie peut atténuer les effets de la fermeture du couvert et permettre le développement du sous-bois, mais nous n'avons pas d'indices que l'effet de l'éclaircie puisse s'étendre sur 8–10 ans. Nous présentons les résultats d'éclaircies expérimentales après 4–5 ans et 8–10 ans dans la forêt nationale de Tongass pour illustrer les effets de l'éclaircie précommerciale (éclaircie versus témoins), de l'âge du peuplement (15–25, 25–35 et 35–50 ans), ainsi que des conditions météorologiques sur la dynamique du sous-bois et la disponibilité de nourriture pour le cerf de Sitka (*Odocoileus hemionus sitkensis* Merriam, 1898). La densité du peuplement affectait négativement la biomasse du sous-bois tandis que la température et la précipitation interagissaient pour augmenter la biomasse. L'éclaircie a eu un effet durable sur le sous-bois : jusqu'à l'âge de 10 ans il y avait deux fois plus de biomasse dans les peuplements éclaircis que dans les peuplements non éclaircis. Nous avons identifié des différences de composition à la suite d'une éclaircie à mesure que la classe d'âge du peuplement augmentait. La nourriture du cerf de Sitka réagissait comme la biomasse mais les différences causées par l'éclaircie s'estompaient avec les scénarios d'augmentation des chutes de neige durant l'hiver, particulièrement dans les peuplements plus vieux. Cette étude aide à comprendre le développement de l'étage dominant et du sous-bois à la suite de traitements sylvicoles dans la forêt pluvieuse tempérée côtière de l'Alaska et a des répercussions sur l'aménagement et des applications pour équilibrer les objectifs à travers les types de forêt. [Traduit par la Rédaction]

Mots-clés : études portant sur la repousse de seconde venue dans la forêt de Tongass, épinette de Sitka (*Picea sitchensis*), pruche de l'Ouest (*Tsuga heterophylla*), système d'évaluation des ressources alimentaires dans l'habitat du cerf — un modèle interactif, diversité du sous-bois.

Introduction

The temperate rain forest of the Pacific Northwest in North America stretches from southcentral Alaska through to British Columbia and as far south as northern California. Cool, wet maritime climate in this region befits mixed forests of Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn ex D. Don), and Alaskan yellow cedar (*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little) in ecosystems that are often driven by gap-scale disturbances (Lertzman et al. 1996; DellaSalla et al. 2011). These Sitka spruce – western hemlock (SSWH) forests in southeast Alaska, United States, provide a wide array of ecosystem services to people

Received 6 August 2019. Accepted 4 November 2019.

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Can. J. For. Res. **50**: 215–225 (2020) dx.doi.org/10.1139/cjfr-2019-0268

on local to global scales, including food, fiber, clean air and water, biodiversity, carbon sequestration, scenic and cultural values, and fish and wildlife (Wipfli et al. 2002; Deal et al. 2014).

Although old-growth stands are typically considered the best habitat for deer, structure and composition in SSWH forests in southeast Alaska are dynamic (Alaback 1982; Schneider and Larson 2017). Prior to the introduction of a timber industry in the 19th century, these SSWH forests were old-growth forests subject to small- to medium-sized disturbances such as avalanches, landslides, wind, insects, and disease (Lertzman et al. 1996; DeGayner et al. 2005; Pearson 2010). Wildfire is notably absent in these forests, which are often too wet to burn or lack ignition sources. Disturbances often range in spatial scale from a single tree to hundreds or even thousands of hectares and in temporal scale from frequent to infrequent: tree-scale disturbances are most common, stand-scale disturbances are infrequent, and landscape-scale disturbances are rare. Over the course of natural stand dynamics, overstory stems growing in gaps or large swaths following disturbance would competitively crowd out understory vegetation until the understory reinitiation, or mature forest stage, when sufficient resources reach the forest floor to stimulate understory redevelopment (Alaback 1982; Oliver and Larson 1996).

Active, even-aged forest management (especially in the 20th century) has likewise been enacted as a disturbance agent through harvesting and thinning SSWH stands, which redistributes resource availability to newly regenerated or retained trees and associated understory species (Hale 2003; Pearson 2010). Forest dynamics following clear-cutting can be quite different than the more frequent gap-scale disturbances (Deal 2007), primarily because of their larger spatial scale. Clear-cut harvests typically result in 40 or more contiguous hectares of dense natural conifer regeneration that competitively shades out understory forbs and shrubs for a century (Alaback 1984). Thinning removes trees and increases subcanopy light penetration, but past studies have documented poor success in maintaining understory response 5–15 years after treatment (Deal and Farr 1994; Tappeiner and Alaback 2007). Opened overstory canopies in managed stands close in according to natural vegetation dynamics following disturbance (Banner and LePage 2008), and further intermediate silvicultural treatments are necessary to defer understory exclusion.

Precommercial thinning in young-growth (i.e., second-growth; regenerated after old growth) stands has the potential to meet multiple management objectives, including effectively improving both timber and understory vegetation and increasing forage for deer throughout the entire stand (Doerr and Sandburg 1986; Cole et al. 2010; Verschuyl et al. 2011; Hanley et al. 2013). Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam, 1898) are a species of major interest in southeast Alaska that thrive where understory forage is available (Wallmo and Schoen 1980; Hanley 1993; Hanley and Brady 1997). Although precommercial thinning is a common management practice in southeast Alaska, widely replicated studies demonstrating decade-long effects of thinning on understory development across stand age classes, especially in light of deer forage needs, are lacking.

In this study, we use an experimental design with a wide geographical footprint and a range of stand ages to characterize understory vegetation from actively managed young-growth stands in southeast Alaska (Crotteau et al. 2020). Our principal research focus was to determine the effects of precommercial thinning and stand age on understory dynamics and deer forage availability. Because our experiments spanned multiple years, we first assessed the relative effects of weather, forest density, and stand age on untreated understory biomass to better understand driving ecological influences and then analyzed the development of understory biomass, composition, and deer forage by treatment (i.e., thinned versus unthinned). We hypothesized that thinning would increase understory biomass, diversity, and deer forage availability because of the understory's improved access to resources beyond that of unthinned stands. We also hypothesized that stand age would dampen understory biomass, diversity, and forage because understories become competitively excluded or suppressed with overstory development. Forest management in southeast Alaska often aims to balance timber production and wildlife needs, and this study is the first to evaluate up to 10-year effects of thinning on deer habitat in young-growth forests with such a widely replicated, geographically extensive study design. We demonstrate the effects of thinning relative to a no-action treatment, which is especially useful to forest managers considering the lasting effects of multiple land-management alternatives.

Methods

Study sites

Much of southeast Alaska is made up of the Alexander Archipelago, large islands separated by narrow channels, where steep slopes and fjords were carved by glaciers that now dominate the mainland interior. The climate is cool and wet, with more precipitation on the western edge of the islands that decreases eastward toward the mainland. Mean monthly temperatures range from around 0 °C in January to around 13 °C in July. There is high local variation in annual precipitation, but rainfall generally ranges from 160 cm further north to 360 cm in the south, plus 90–220 cm of snowfall during winter months, varying locally. Forested areas are primarily dominated by western hemlock and Sitka spruce, with western red cedar south of 56 °N and Alaskan yellow cedar throughout the region. Logging has historically been more common in the southern portion of the region; therefore, a high proportion of the region's young-growth stands are located in the south.

This study uses a subset of the expansive Tongass-Wide Young-Growth Studies (TWYGS) (McClellan 2008; Hanley et al. 2013). TWYGS is a randomized and replicated set of similarly designed silvicultural experiments with sites located across the Tongass National Forest (Fig. 1). Three experiments were designed to evaluate the effects of precommercial thinning to improve timber and wildlife habitat in young-growth stands of ages 15–25, 25–35, and 35–50 years old (Table 1). Although precommercial thinning is typically practiced in stands less than 25 years old, we considered thinning in a variety of nonmerchantable age classes and considered them all "precommercial." We focus on each experiment's basic thinning treatment (e.g., excluding treatments with pruning) and paired untreated control to demonstrate the most salient effects of thinning. Target residual densities reduced with stand age class from 549 trees·ha^{-1} in the 15–25 year age class to 420 trees·ha^{-1} in the 25–35 year age class and 203 trees·ha^{-1} in the 35–50 year age class. Although prescribed densities were not identical across age classes, treatment severity was similar, retaining approximately 9.1%–10.6% of trees per stand (calculated using control densities 4–5 years after treatment, in the absence of immediate posttreatment data). Thus, although there is some confounding of age class and treatment in this design, we expect it to be minor, and differences will most likely be due to age class.

For each experiment, 13–18 installations were established (Table 1), each with a randomly assigned thinned and control unit. Installations were constrained to low-elevation (<365 m), productive timber stands that were naturally regenerated following clear-cutting but had received no precommercial thinning prior to treatment. Efforts were made to select installations with relatively uniform stand productivity, density, and composition at the time of treatment. When possible, all treatment units were placed within the same operational harvest unit and separated by untreated buffers. Treatment units ranged in size from 1.9 to 84.8 ha. Additionally, many had a south-facing aspect and were within areas likely frequented by Sitka black-tailed deer in winter.

Fig. 1. Locations of study sites: 50 installations in three experiments spread throughout the Tongass National Forest (NF). All but two installations are located on islands. TWYGS, Tongass-Wide Young-Growth Study. Map data: USDA Forest Service geographic information system (GIS). Map created using ArcMap 10.5.1 (Esri, Redlands, Calif., USA). [Color online.]

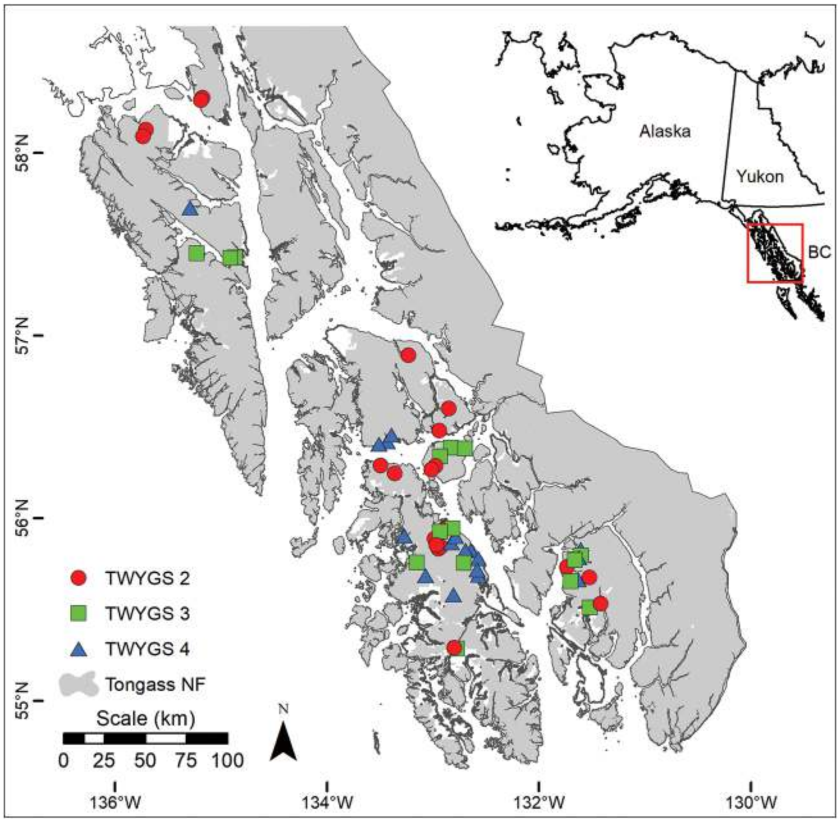


Table 1. Experimental design of Tongass-Wide Young-Growth Studies (TWYGS) 2, 3, and 4.

TWYGS experiment	Age class (years)	Prescribed thinning intensity (trees·ha^{-1})	No. of installations	Mean unit area (ha) (SE)	Year thinned	Measurement dates
2	15–25	549	18	11.3 (0.1)	2002	2007, 2012
3	25–35	420	13	12.4 (0.5)	2002–2003	2008, 2013
4	35–50	203	17	3.1 (0.02)	2006	2010, 2014

Note: Each experiment tested a thinning intensity on a different young-growth age class. One stand in TWYGS 4 was age 60 at time of treatment, but the remaining stands were all less than 50 years old. SE, standard error.

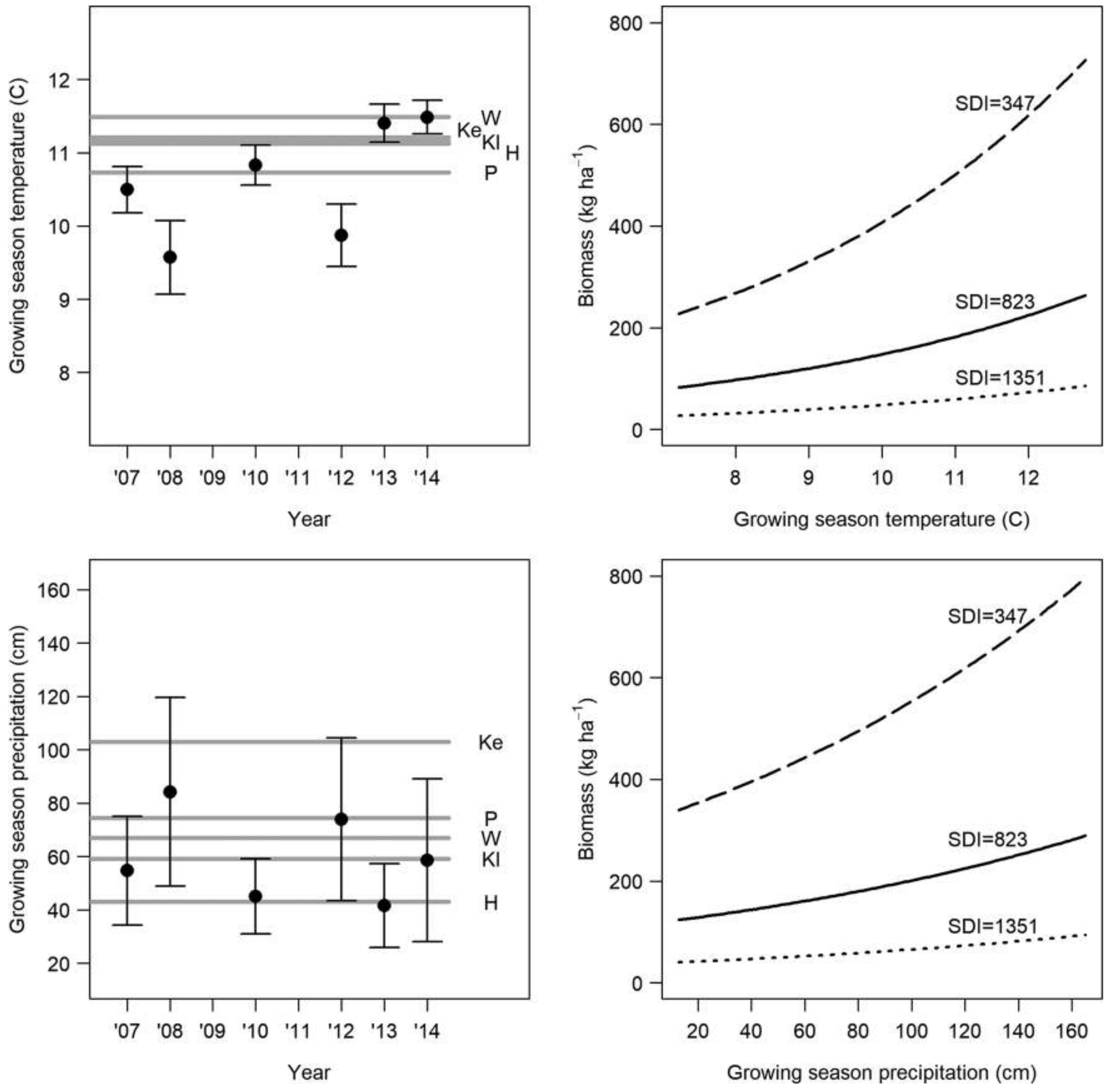
Data collection

A grid of four or five systematically located, 0.05 ha permanent plots were installed in each unit. Plots were established at least 25 m from the treatment boundary to reduce edge effects. Overstory and understory data were collected from each TWYGS experiment on a rotating schedule, establishing posttreatment data sets from two sample dates on either a 4-year or 5-year cycle (Table 1).

We assessed unit overstories by recording status (live or dead), species, diameter at breast height (DBH; breast height = 1.37 m), and height for all standing trees ≥2.5 cm DBH within each thinned plot. In most control plots, it was impractical to measure all trees because of high density (>3000 trees·ha^{-1}), and a grid of nine 9 m^2 subplots was established to sample overstory attributes. We then measured canopy cover on each plot by taking a photograph from plot center at breast height using a fish-eye lens on a Nikon D5000 digital camera (Nikon, Tokyo, Japan); cover was estimated using Gap Light Analyzer (years 2007–2008; Frazer et al. 1999) or HemiView (years 2010–2014; Delta-T Devices, Cambridge, UK; Rich et al. 1999). Canopy cover estimates from these two programs are comparable in these young-growth stands (J. Crotteau, personal observation).

Field crews visually identified and estimated horizontal cover of each vascular understory species (≤1.37 m tall) in sixty 1 m^2 quadrats per unit, which were distributed evenly and systematically across permanent plots, at least 6 m from plot centers to avoid trampling. Field crews used 1 m × 1 m square frames with 10 cm demarcations to estimate cover and were calibrated during a training period with experienced staff. Nonwoody understory biomass (hereafter referred to as simply "understory biomass"; in kilograms per hectare) was estimated for these quadrats using regressions that we developed for cover to biomass; woody biomass was not estimated. We destructively sampled understory biomass (i.e., dry mass) for each species by clipping and weighing the nonwoody materials from plants across a range of targeted cover values (1%–100% cover, by ~10% increments). Biomass samples were located within the treatment units but outside the permanent plots and only at installations connected to the Prince of Wales road system for access to drying ovens. After oven-drying plant materials at 100 °C for at least 24 h, we developed species-specific regressions of cover to biomass for current annual growth of each forage type (i.e., total aboveground plant for herbs, leaves, and nonwoody twigs for shrubs and trees) and sample year, where n ranged from 3 to 18 samples. Regression equations had a mean

Fig. 2. Growing season (April–August) weather data across measurement years (left panels) and weather predictor effects on understory biomass (right panels). Left panels display mean (and 1 standard error) temperature (top left) and total precipitation (bottom left) from five weather stations in southeast Alaska. Gray lines are 30-year normals (1981–2010), labeled by weather station (from north to south: H, Hoonah; P, Petersburg; W, Wrangell; Kl, Klawock; Ke, Ketchikan). Right panels show model predictions of total understory biomass across the sampled range of temperature (top right) and precipitation (bottom right) for three levels of stand density index (SDI): first quartile of observations (SDI = 347), mean of observations (SDI = 823), and third quartile of observations (SDI = 1351). For simplicity, values were predicted using the mean values of other predictors in the model (see Table 3).



R^2 of 0.85 (median of 0.88) but ranged from 0.07 to 1.00. For uncommon species that lacked sufficient observations, we used local regression equations (M. Hanley, unpublished data). Understory canopy and biomass data were collected from mid-June through mid-August to coincide with peak understory development.

We accessed weather data from airport weather stations nearest each installation through the National Centers for Environmental Information Local Climatological Data portal (www.ncdc.noaa.gov/cdo-web/datatools/lcd). We used mean growing season (April–August) temperature and precipitation associated with each measurement year to assess influence of weather on biomass (Fig. 2, left panels).

Analytical methods

We calculated stand density and stand density index (SDI; Reineke 1933) for each treatment unit (thinned and control) to evaluate the effects of the treatment on the stand density and understory dynamics. All cover and biomass data were analyzed at the unit level. Understory biomass for each species was calculated using regressions of cover to biomass and then summed by functional class in each unit, where functional classes included ferns, forbs, graminoids, shrubs, and understory trees.

We evaluated total understory biomass (i.e., nonwoody components from all plants) in control units alone to account for baseline annual variation in biomass due to weather, stand density, and age; treated units were excluded to simplify interpretation of the natural process. We fit a linear mixed-effects model to log-transformed understory biomass using lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) in R (R Core Team 2016). Fixed effects included interactions between mean temperature and total precipitation, SDI, age when experiment was implemented, and measurement (i.e., first measurement at 4–5 years after treatment and second measurement at 8–10 years after treatment).

Table 2. Mean (and SE) overstory characteristics of TWYGS experiments by measurement.

Experiment, age class	TWYGS 2, 15–25 years				TWYGS 3, 25–35 years				TWYGS 4, 35–50 years			
Treatment	Control		Thinned		Control		Thinned		Control		Thinned	
Measurement	1	2	1	2	1	2	1	2	1	2	1	2
Density (trees·ha^{-1})	5223 (795)	5919 (677)	514 (25)	560 (25)	3966 (461)	3516 (504)	439 (22)	425 (17)	2237 (340)	2144 (298)	167 (12)	162 (11)
Canopy cover (%)	88.0 (1.7)	84.1 (1.7)	68.3 (3.0)	72.3 (2.5)	88.8 (1.9)	91.8 (1.2)	79.3 (2.1)	85.5 (1.6)	89.7 (1.1)	92.3 (0.5)	67.1 (2.1)	82.2 (1.8)
SDI	760 (88)	1189 (96)	208 (21)	371 (25)	1294 (139)	1586 (165)	397 (54)	519 (59)	1436 (80)	1540 (111)	327 (22)	384 (24)
Height (m)	11.9 (0.1)	12.7 (0.1)	11.0 (0.0)	12.3 (0.0)	16.3 (0.3)	17.0 (0.3)	16.9 (0.4)	18.1 (0.4)	20.4 (0.2)	21.8 (0.2)	22.9 (0.2)	24.1 (0.3)

Note: For TWYGS 2 and 3, measurement 1 was taken 5 years after treatment and measurement 2 was taken 10 years after treatment. For TWYGS 4, measurement 1 was taken 4 years after treatment and measurement 2 was taken 8 years after treatment. Height refers to all trees with diameter at breast height (DBH; breast height = 1.37 m) greater than 15 cm. SDI, stand density index.

Installation (site) was treated as a random effect to account for repeated measures. Covariates were scaled by their mean and standard deviation to more easily assess importance of estimated coefficients, which we supplemented by reporting coefficient *p* values. We calculated and inspected variance inflation factors (VIFs) of model predictors to ensure that multicollinearity was not a problem. After fitting the model, we used the mean values of covariates to plot and assess partial predictions from the most significant covariates: temperature, precipitation, and SDI.

Once we clarified the relative effects of weather, stand density, and age on understory biomass in the control units, we developed a second model to test the effect of thinning treatments on understory biomass. This model's fixed-effect factors included experiment age class (i.e., 15–25, 25–35, and 35–50 years), unit thinning status (i.e., thinned or unthinned control), and the measurement (first at 4–5 years or second at 8–10 years). Both this treatment model and the previously described control model were tested against their respective null models using the likelihood ratio test and Akaike's Information Criterion (AIC). Here, we used analysis of variance (ANOVA) to interpret treatment effects after verifying that variances by factors were homoscedastic using Levene's test. Additionally, we calculated the ratio of biomass in thinned units to the annual mean biomass in control units to further evaluate understory response to thinning.

Species composition is an important ecological attribute of understory development. We used rank-abundance curves from both measurements to understand how thinning affects species evenness and richness within and across experiments. Rank-abundance curves demonstrate compositional diversity, where the length of the line represents species richness and the horizontal flatness of the line represents species evenness. We also summarized biomass by functional class to understand how treatment affects understory structure and functional composition over time. The biomass of each functional class was compared across experiments and measurements using Dunnett–Tukey–Kramer's post hoc tests with an alpha of 0.05 using the DTK package in R (Lau 2013), which accounts for the unequal variance across groups that we encountered in these unscaled biomass composition analyses. Finally, we isolated and summarized the species with >10% relative cover in each treatment type to evaluate how treatment affects dominant understory species.

To quantify the habitat value of treatment units for Sitka black-tailed deer, we used the Forage Resource Evaluation System for Habitat deer (FRESH-deer) model (Hanley et al. 2012). This model calculates "deer days" per hectare using established values for forage nutritional quality and deer metabolic requirements, where 1 deer day is defined as the food resources necessary to sustain one adult female deer for 1 day. FRESH-deer does not consider herbivore–plant interactions, deer population dynamics, or physical accessibility through stands, so the model output should be simply understood as the potential forage at a single point in time. The model output, therefore, represents an upper bound on the number of deer a habitat can support with currently available forage as the limiting factor. These results provide a quantitative forage value to compare among treatment alternatives and should not be interpreted as an absolute representation of how many deer a stand supports (Hanley et al. 2012).

We used the FRESH-deer model to calculate deer days for all thinned and control units in two summer and six winter scenarios. In the summer scenarios, the model uses all available understory biomass but different metabolic requirements, with one assuming a solo female (maintenance) and the other assuming a mother with a fawn (maintenance + lactation). In the winter scenarios, forage nutritional values reflect only the plant biomass that persists through the winter and that remains unburied by snow, and the metabolic requirements are changed to represent deer winter needs. FRESH-deer uses a nonlinear relationship between canopy cover and forest-floor snow depth to determine forage availability; we modeled six snowfall scenarios ranging from 0 to 100 cm to demonstrate a range of winter forage conditions based on snowfall. We use "deer forage" as the integration of edible understory biomass and nutritional content, as represented by FRESH deer days per hectare. Deer forage in each scenario was compared across experiments and measurements using Dunnett–Tukey–Kramer's post hoc tests.

Results

Overstory characteristics

Up to a decade after thinning, stand density metrics (trees per hectare, canopy cover, and SDI) continued to remain below those of control units, per original treatment prescriptions (Table 2). Stem density in control units was high; in the 25–35 and 35–50 year age classes, density declined as age increased, which is indicative of competitive mortality due to stem exclusion. Tree density in thinned units approximated retention targets in the 15–25 and 25–35 year age classes (within 10% of 549 and 420 trees·ha^{-1}, respectively), but stands in the 35–50 year age class were 18% less dense than the prescription (203 trees·ha^{-1}). Unlike tree density, relative density (SDI) increased in control units across treatments as stand age increased. This illustrated that tree diameter growth in the control increased relative density more than competitive mortality reduced it. SDI increased between measurements in thinned units at a rate similar to that of the control units. In control units, canopies were nearly closed, with a mean cover of 89%. In thinned units, mean canopy cover was 19% lower 5 years after treatment than in the control units but increased at 10 years to only 11% lower than in the control units as individual tree crowns expanded and occupied the available growing space.

Understory biomass

Our control understory biomass model showed that relative density (SDI) and weather (temperature × precipitation interaction) significantly affected the log of biomass (Table 3; Fig. 2). Coefficients indicate a decline in understory biomass as SDI increased, whereas biomass increased with wet, warm weather. Increases in temperature and precipitation (across the range of

Table 3. Coefficient table from the linear mixed-effects model of total understory biomass in control units.

Variable	Estimate	SE	df	t	Pr (>|t|)
(Intercept)	3.68	0.24	57.87	15.47	**<0.001**
Mean temperature (°C)	0.24	0.15	45.74	1.61	0.115
Total precipitation (cm)	0.29	0.16	72.65	1.84	*0.070*
Relative density (SDI)	–0.82	0.21	67.67	–3.83	**<0.001**
Age (years)	–0.25	0.23	46.64	–1.06	0.295
Measurement 2	0.28	0.25	54.55	1.12	0.269
Temperature × precipitation	0.29	0.12	51.09	2.50	**0.016**

Note: Response variable is the natural logarithm of biomass (kg·ha^{-1}). Degrees of freedom (df) were calculated per Satterthwaithe's method, and the model was fitted by restricted maximum likelihood (REML). Measurement 2 was taken 8–10 years after treatment. Values in boldface type indicate $p < 0.05$; values in italic type indicate p = 0.05–0.10. ×, interaction.

observed values) both increased biomass, but biomass increased substantially more with SDI reductions, demonstrating the defining effect that overstory competition has on the understory (Fig. 2). Age did not have a significant effect on understory biomass, though we do note that age and SDI were slightly correlated (Pearson's correlation coefficient = 0.36, $\text{VIF}_{\text{Age}} = 1.3$, $\text{VIF}_{\text{SDI}} = 1.5$). The control model was a significant improvement upon the null model ($\Delta\text{AIC} = 27$, $\chi^2_{[6]} = 38.7$, $P < 0.001$). Weather was fairly similar, but SDI increased substantially (56%) across the two measurements in the 15–25 year age class (Table 2), corresponding to a decrease in understory biomass. The opposite occurred in the 35–50 year age class, in which SDI increased by only 7% but precipitation was 60% higher 8 years after treatment than 4 years after treatment, corresponding to increased biomass.

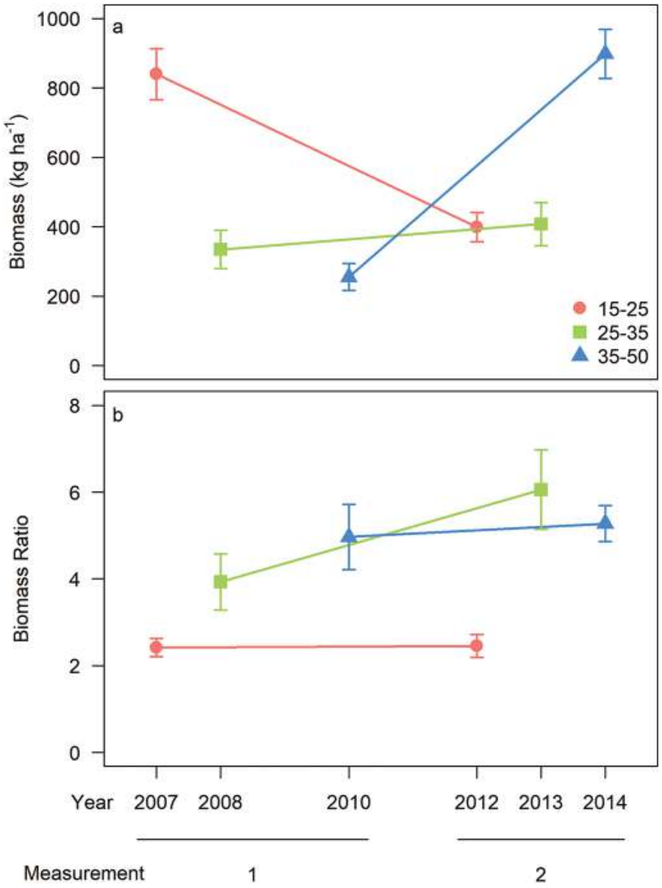
Thinned units had two to six times as much biomass as control units, which was consistent across weather-driven low and high understory biomass years (Fig. 3), depending on the experiment. Our treatment model showed that total biomass varied significantly by age class and thinning and was marginally different by measurement (Table 4). This showed a consistent increase in understory biomass with thinning that varied slightly by age class and increased with time since thinning. The treatment model was a significant improvement upon the null model ($\Delta\text{AIC} = 125.1$, $\chi^2_{[6]} = 137.06$, $P < 0.001$).

Understory composition

Unlike total understory biomass, understory diversity and composition were not strongly affected by thinning in all experiments. Rank-abundance curves (Fig. 4) show that control units and thinned units in the youngest age class had similar species richness (horizontal distance) and evenness (slope of curve) across the measurement period. This trend was also evident in the 25–35 year age class at the 5-year measurement, but 10 years after thinning, there was a drop in species richness and evenness in the control units. In the oldest age class, thinned units had greater species richness and evenness than the control units at both visits, with this trend slightly clearer at the second visit (8 years). Overall, the rank-abundance curves for the two younger age classes were very similar, whereas the curves for the 35–50 year age class stood out with lower richness and higher evenness.

Although biomass in each functional class largely followed total understory biomass, functional class proportion of total biomass varied in this study (Table 5). Shrubs were the most abundant class in all treatments, representing 55%–75% of biomass in the younger age classes and 40%–50% of biomass in the oldest. In the younger age classes, shrubs were an even greater proportion of biomass in thinned units compared with control units. Ferns comprised 10%–20% of total biomass in the younger age classes but 20%–35% in the oldest. Forbs comprised 5%–20% of biomass in all treatments, representing a greater proportion of biomass in control units compared with thinned units in the 15–25 and 35–50 year age classes. Understory trees (i.e., materials below breast height) were 5%–30% of total biomass in each treatment. Trees made up a greater proportion of biomass in control units compared with thinned units in the 25–35 year age class, but in the 35–50 year age class, the reverse was true. Additionally, trees in the oldest age class comprised a greater proportion of biomass at the 8-year measurement than at the 4-year measurement.

Fig. 3. Response of understory biomass in thinned units 8–10 years after thinning. Panel *a* shows the biomass in thinned units of each experiment. Panel *b* shows the ratio of biomass in the thinned unit to the mean biomass of control units measured in that year. [Color online.]



Isolating the most abundant species by cover in each treatment (Table 6) further supports the trends seen by functional class. Shrubs dominated in the younger age classes, as *Vaccinium ovalifolium* Sm. was the most abundant species in all but one instance in which *Rubus spectabilis* Pursh was more abundant. In the oldest age class, however, species from other functional classes displaced *Vaccinium ovalifolium* dominance. *Tiarella trifoliata* L. was the only forb with more than 10% cover and helped characterize compositional uniqueness in the control units in the 35–50 year age class. That class was also characterized by a consortium of ferns, and by the second visit to its thinned units, understory western hemlock (*Tsuga heterophylla*) was the most abundant species.

Deer habitat

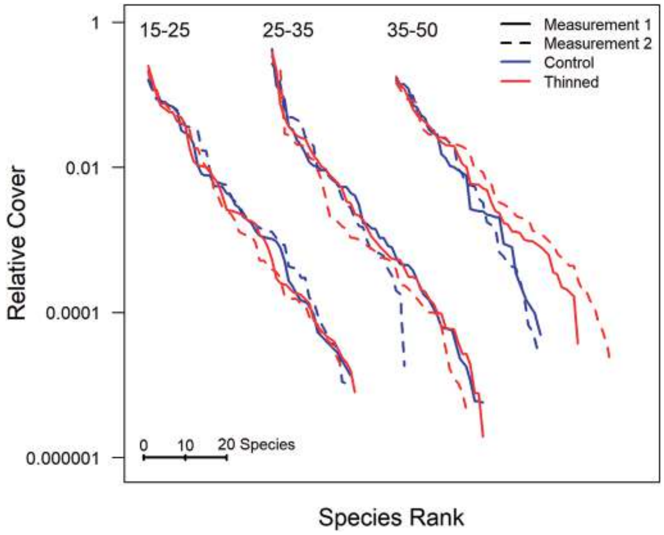
Summer deer forage (i.e., maintenance; in deer days per hectare) closely followed the trends described in our analysis of total understory biomass (Table 7). There was greater deer forage in thinned units than in the unthinned control, particularly in the oldest age class. The first visit to the 15–25 year age class and the second visit to the 35–50 year age class had the highest deer forage values (following weather-driven fluctuations in understory bio-

Table 4. Type III analysis of variance (ANOVA) of the linear mixed-effects model of understory biomass in thinned and control units.

Factor	df	Denominator df	*F*	Pr (>*F*)
Age class (15–25, 25–35, or 35–50 years)	2	41.00	5.38	**0.008**
Thinning (yes or no)	1	132.21	193.18	**<0.001**
Years after treatment (measurement 1 or 2)	1	135.67	2.94	*0.089*
Experiment × thinning	2	132.21	1.41	0.248

Note: Response variable is the square root of biomass (kg·ha^{-1}). Denominator degrees of freedom were calculated per Satterthwaithe's method, and the model was fitted by REML. Values in boldface type indicate $p < 0.05$; values in italic type indicate $p = 0.05$–0.10.

Fig. 4. Rank-abundance curves of TWYGS experiments (TWYGS 2, 15–25 years; TWYGS 3, 25–35 years; TWYGS 4, 35–50 years). Each curve represents the aggregate species composition of all installations. Measurement 1 was taken 4–5 years after treatment, and measurement 2 was taken 8–10 years after treatment. [Color online.]



mass), whereas the other measurements had similar deer forage values. Combining all treatments, summer forage for lactating deer was 45%–63% lower than single-deer maintenance needs because of increased nutritional requirements.

Deer forage analysis of the oldest age classes also followed the overall biomass trends in no-snow winter scenarios, but there was some variation in the thinned units of the youngest age class at the 10-year measurement (Table 7). There, the understory was composed primarily of species and components that persist over the winter, resulting in only a minor decrease in total available biomass in the winter. However, deer nutrition requirements are lower in winter than in summer, resulting in more available forage in the no-snow winter scenario (295.6 deer days·ha^{-1}) than in the summer maintenance scenario (265.7 deer days·ha^{-1}).

As we increased snowfall in the FRESH-deer model, overwinter forbs were "covered up" and available deer forage decreased rapidly; only shrub twigs and conifer current annual growth were considered available to deer (Table 7). From the no-snow scenario to the 20 cm snowfall scenario, deer forage decreased by a mean of 76%. The smallest forage decrease in this step was in the second measurement of thinned units in the youngest age class, in which only 66% of forage was buried by the first 20 cm of snow. The two measurements of thinned units in the oldest age class had the largest decrease, losing 85% of available forage from the no-snow to 20 cm snowfall scenarios. As we continued to increase snowfall, forage in all units decreased by a mean of 70% per 20 cm of snowfall. In the 100 cm snowfall scenario, remaining forage was highest in the youngest age class (second measurement in the thinned units), which along with the adjacent unthinned units had only 85% of overwinter forage covered. Unthinned units in the oldest age class had the least available forage with 100 cm snowfall: 99% of overwinter forage was covered or unavailable.

Discussion

We found that precommercial thinning in stands across three age classes increases understory biomass and forage through 10 years after treatment in young-growth SSWH forests in southeast Alaska. These results suggest that simultaneously meeting resource objectives for improved deer forage and timber production is possible, especially in younger stands in which understory species composition provides valuable deer nutrition. Finally, we note that the contrast between these thinned and unthinned stands informs effectiveness and longevity of treatment in a simple and pragmatic way.

Effects of climate, stand density, and age on understory

Although our motivating research question focused on understanding the effects of thinning on the forest understory, we began our research by demonstrating the relative influence of weather, stand density, and age on understory biomass in the untreated control units, which form the undulating backdrop in which we later evaluate treatment effects. We confirmed that both weather and stand density moderate understory biomass, whereas the influence of stand age was not as important as that of density. This differed from our second hypothesis, which assumed that age was the driver of total biomass. Whereas stand density increased with age and measurement, incrementally limiting understory biomass in this study, weather varied across years and caused unexpected shifts in biomass. Namely, the decrease in biomass we observed in the 15–25 year age class (the most open control overstories by canopy cover and SDI) over time was in direct contrast to the increase in biomass in the 35–50 year age class (the most dense control overstories), highlighting that the combination of warm temperatures and precipitation moderate the limiting effects of overstory competition. In drier forest ecosystems, Strahan et al. (2015) and Crotteau et al. (2020) caution that the climate signature from poorly or highly productive years may confound understanding of long-term understory dynamics. Weather is a major determinant in plant growth, specifically the interaction among light, temperature, and moisture (Anderson et al. 1969). Even in well-regulated maritime climates, variability in temperature and moisture moderate primary productivity and respiration (Curiel Yuste et al. 2003; Fukuzawa et al. 2013), so it is no surprise that annual variability of these weather attributes modulates understory biomass. Likewise, we expected that stand density would competitively moderate understory vegetation because of increasing overstory competition associated with natural stand dynamics (Oliver and Larson 1996).

In addition to confirming ecological drivers to biomass development in young, untreated SSWH stands, we quantified dynamics in understory life-form composition, principal species, and associated deer forage. These contributions provide valuable depth to the understanding of myriad young-growth hectares across southeast Alaska. Composition was similar to expectations from this phase of stand development, especially per Cole et al.

Table 5. Mean biomass (kg·ha⁻¹) per functional class in all TWYGS experiments.

Experiment, age class	TWYGS 2, 15–25 years				TWYGS 3, 25–35 years				TWYGS 4, 35–50 years			
Treatment	Control		Thinned		Control		Thinned		Control		Thinned	
Measurement	1	2	1	2	1	2	1	2	1	2	1	2
kg·m⁻²												
Ferns	47.6bcd	31.2bcd	93.4b	64.1b	9.1d	11.8d	51.6bc	54.5b	12.1cd	36.2bcd	86.2b	214.6a
Forbs	61.7a	21.0abcd	57.5ab	35.3abc	8.0acd	6.8ad	32.5abcd	19.8abcd	9.6acd	28.9abcd	22.3abcd	49.7abc
Graminoids	1.3a	0.2a	4.1a	1.1a	0.0a	0.0a	3.9a	1.8a	0.0a	0.3a	5.4a	8.4a
Shrubs	205.9bcde	95.3cef	625.0a	267.5bcd	51.8ef	38.0f	220.9bcde	290.7bc	25.7f	68.8cef	103.1cef	377.7b
Trees	31.0bcd	14.7bcdef	59.7b	31.0bcde	16.2bcdef	10.7bcdef	25.8bcdef	41.1bc	3.9bdf	36.0bc	38.2bc	247.4a
Total	47.6bcd	31.2bcd	93.4b	64.1b	9.1d	11.8d	51.6bc	54.5b	12.1cd	36.2bcd	86.2b	214.6a
% of total												
Ferns	14%	19%	11%	17%	11%	18%	15%	13%	24%	21%	34%	24%
Forbs	18%	13%	7%	9%	9%	10%	10%	5%	19%	17%	9%	6%
Graminoids	0%	0%	0%	0%	0%	0%	1%	0%	0%	0%	2%	1%
Shrubs	59%	59%	74%	65%	61%	56%	66%	71%	50%	40%	40%	42%
Trees	9%	9%	7%	8%	19%	16%	8%	10%	8%	21%	15%	28%

Note: Tukey–Kramer letters refer to variation within the functional class across experiment, treatment, and measurement (i.e., by row). For TWYGS 2 and 3, measurement 1 was taken 5 years after treatment and measurement 2 was taken 10 years after treatment. For TWYGS 4, measurement 1 was taken 4 years after treatment and measurement 2 was taken 8 years after treatment.

Table 6. Mean absolute cover (%) of the dominant understory species (top decile of total understory composition) within each TWYGS experiment and measurement year.

Experiment, age class		TWYGS 2, 15–25 years				TWYGS 3, 25–35 years				TWYGS 4, 35–50 years			
Treatment		Control		Thinned		Control		Thinned		Control		Thinned	
Measurement		1	2	1	2	1	2	1	2	1	2	1	2
Forb	*Tiarella trifoliata*									1.7	2.7		
Fern	*Athyrium filix-femina*										3.1		9.7
	Dryopteris expansa									2.1	2.7	5.7	
	Gymnocarpium dryopteris									1.7	4.4	3.8	
Shrub	*Menziesia ferruginea*	5.2		7.4	7.9	2.5	2.0		18.1				
	Rubus spectabilis		3.1	12.1	7.6		3.0	14.9	28.0			4.4	12.0
	Vaccinium ovalifolium	9.2	4.3	18.6	13.8	9.6	3.8	26.4	18.2	2.8	3.7		
Tree	*Tsuga heterophylla*	4.9				3.0							14.9

Note: For TWYGS 2 and 3, measurement 1 was taken 5 years after treatment and measurement 2 was taken 10 years after treatment. For TWYGS 4, measurement 1 was taken 4 years after treatment and measurement 2 was taken 8 years after treatment.

Table 7. Mean deer forage (deer days·ha⁻¹) in eight scenarios.

Experiment, age class	TWYGS 2, 15–25 years				TWYGS 3, 25–35 years				TWYGS 4, 35–50 years			
Treatment	Control		Thinned		Control		Thinned		Control		Thinned	
Measurement	1	2	1	2	1	2	1	2	1	2	1	2
Summer scenario												
Maintenance	266.7bc	114.7bcdef	666.7a	265.7bcd	65.0cef	46.7cf	271.7b	244.1bcd	37.0cf	114.4bcdef	187.2bcde	609.5a
Lactation	142.9abc	62.9cdef	268.5ab	118.3cd	30.0cef	20.3cf	126.2bcd	89.2cdef	18.3cf	52.6cdef	103.4cde	280.0a
Winter scenario												
No snow	179.1abcd	87.2cd	457.0a	295.6ab	35.9d	24.6d	174.2abcd	117.3bcd	33.4d	88.7bcd	105.0bcd	291.4abc
20 cm snowfall	57.9abc	27.6bcde	124.4a	100.8ab	11.8cde	5.2ce	46.3abc	25.1bcde	10.4cde	17.4cde	15.5cde	42.2abcd
40 cm snowfall	43.9abc	25.0abc	79.6ab	84.8a	9.2bc	3.9c	32.6abc	19.6abc	7.5c	11.1bc	10.0bc	27.6abc
60 cm snowfall	32.8ab	21.1ab	51.8ab	68.8a	7.1b	3.0b	23.3ab	15.3ab	5.1b	7.1b	6.5b	17.5ab
80 cm snowfall	24.4ab	17.2ab	31.2ab	58.7a	5.5b	2.3b	16.2ab	11.8b	3.4b	4.2b	3.9b	10.3b
100 cm snowfall	17.3ab	13.3ab	14.7ab	43.5a	4.2b	1.7b	10.2ab	8.9b	1.9b	2.0b	1.8b	3.9b

Note: Maintenance, single doe; lactation, doe plus one fawn (accounts for increased nutritional requirements). Winter scenarios account for overwintering forage and winter nutrition requirements. Tukey–Kramer letters refer to variation within the scenario class across experiment, treatment, and measurement (i.e., by row). For TWYGS 2 and 3, measurement 1 was taken 5 years after treatment and measurement 2 was taken 10 years after treatment. For TWYGS 4, measurement 1 was taken 4 years after treatment and measurement 2 was taken 8 years after treatment.

(2010), who documented understories in stands 16–17 years old upon treatment, and Alaback (1982), who documented understories in stands up to 300 years old. Shortly after disturbance (i.e., clear-cutting) and while shrub and conifer competition are still relatively short, forbs and ferns are abundant, particularly in young-growth stands similar to ours (Cole et al. 2010). Alaback (1982) found that shrub biomass disproportionately dominated forest understory composition for the first 50 years following disturbance, after which the relative abundance of ferns began to balance understory biomass. We corroborate Alaback's (1982) observations, demonstrating the transition in dominant understory species from *Menziesia ferruginea* Sm., *Rubus spectabilis*, and *Vaccinium ovalifolium* in our youngest untreated stands (15–25 years) to forb and fern species in the oldest stands (35–50 years). This transition in understory dominance with stand age from tall shrub to low herb species has a notable impact on deer forage, which quickly drops to less than 20 days as low plants are covered with winter snowfall (Hanley et al. 2012). Although total understory biomass (including woody stems) has been reported in southeast Alaska and other anecdotal evidence suggests a quick transition from an abundance to dearth of forage in untreated stands, no other study has quantitatively demonstrated the rapid decline in nonwoody, deer-relevant forage availability by stand age that we present. This expected loss of understory forage reiterates the initial justification for this study and provides the context for active management to "improve" upon natural vegetation dynamics by thinning in multiple-use forests.

Effects of precommercial thinning on understory biomass

The primary result of our study is that simple, age-appropriate precommercial thinning effectively increases understory biomass and improves compositional diversity over the no-action alternative for young SSWH stands in southeast Alaska. In the 15–25 (TWYGS 2), 25–35 (TWYGS 3), and 35–50 (TWYGS 4) year age classes, thinning delayed overstory canopy closure and released existing understory flora, delaying the stem exclusion and depauperate understory phase of even-aged stand development. This lined up well with our first hypothesis that thinning improves understories by increasing resource availability. The ratio of biomass in thinned units to the mean biomass in unthinned stands that we reported (i.e., two to six times more biomass) is a conservative estimate: the ratio denominators were averaged across installations within the measurement year rather than the value for an installation's unthinned unit. We did this because biomass was nearly nonexistent in some of the unthinned stands in our study, which caused the ratio to approach infinity. Therefore, the method we chose offers more stable (averaged) estimates of biomass in thinned versus unthinned stands but masks the very stark differences between thinned stands that have an intact understory and some neighboring unthinned stands that have none. Both our biomass ratio and biomass treatment model show that the forest understory is kept intact and even enhanced by thinning through 8–10 years after treatment. Past work in southeast Alaska (Alaback 1984; Doerr and Sandburg 1986; Deal and Farr 1994; Cole et al. 2010; Hanley et al. 2013) and in the lower Pacific Northwest (e.g., Lindh and Muir 2004; He and Barclay 2011) gave us reason to expect these effects, but the decade-long intensity of understory response across stand age classes was largely uncharacterized before this study. Although our model identified that the general effect of thinning was greater than the specific effects of the three experiments on understory biomass, biomass was greatest in the youngest age class (15–25 years). This clearly indicates that early precommercial thinning maximizes understory biomass production by reducing the amount of time that the forest understory has to endure canopy closure (Cole et al. 2010) before low subcanopy light levels and competition have lasting negative effects on the understory's ability to respond to treatment.

The age classes are most notably distinct from each other when considering understory life-form and species diversity. The 15–25 and 25–35 year age classes had very similar understory composition, both between thinned and unthinned stands. Similarities appeared to hold fast until a decade following treatment in the 25–35 year age class, at which time understory diversity in unthinned stands decreased and compositions diverged. As we identified in our assessment of understory biomass dynamics in untreated stands, understory communities appear to shift after age 35. The lagged (i.e., 10-year) divergence among understories of treated and untreated stands in the 25–35 year age class (Fig. 4) suggests that precommercial thinning prior to age 40 is pivotal to maintain existing, diverse, early-seral understory communities (similar to hypothesis formed by Cole et al. (2010)). Following thinning, understory communities in the oldest stands (35–50 years) also diverged from unthinned communities. In fact, among the experiments in the three age classes, those thinned and unthinned communities were the most compositionally distinct; however, the relative abundance of ferns across the oldest age class suggests that thinning releases a later-seral understory community (ferns associated with old growth in Hanley and Brady (1997)) rather than the early-seral, postdisturbance community that was released in the younger age classes. In these SSWH forests, ferns appear to better endure heavy overstory competition compared with flowering plants. We also observed a substantial amount of conifer regeneration by the second measurement to the oldest stands, suggesting that (*i*) the pretreatment understory was not vigorous enough to hamper conifer regeneration; (*ii*) there was abundant advance regeneration prior to treatment; (*iii*) the prescription removed too many overstory trees, which stimulated regeneration; or (*iv*) weather and seed source aligned sufficiently to produce a region-wide flush of western hemlock (Deal and Farr 1994; Giesbrecht et al. 2017). Deal and Farr (1994) and Deal (2001) found that conifer regeneration, especially western hemlock, had a long-term negative effect on understory development; therefore, silvicultural actions that do not stimulate hemlock regeneration are advantageous for the greater understory community.

This study shows that precommercial thinning and age class influence understory abundance and composition, which in turn drive deer forage availability (Doerr and Sandburg 1986; Cole et al. 2010; Hanley et al. 2013). Weather variability, inherent understory variability, and our low-power pairwise statistical tests all limited the detection of statistical differences due to treatment. Although deer forage was generally greater in thinned units than in unthinned units, statistically significant differences were limited to the youngest and oldest stands (i.e., not the 25–35 year age class). Furthermore, only the youngest stands had significantly greater deer forage due to thinning in scenarios that incorporated snowfall; forage in the thinned stands of the 15–25 year age class was also greater than in those of the older classes. This suggests that the compositional mix of tall shrub biomass (especially *Vaccinium ovalifolium*) associated with the early-seral vegetation provides better nutrition or accessibility for deer than the vegetation assemblage that responded to thinning in older young-growth stands (Hanley et al. 2012). This has major implications in managing for deer habitat: treatment timing, or the stage of stand development, is important. Although typical precommercial thinning strategies in older stands (>25 years) may yield similar functional results in the understory (i.e., substantial understory biomass redevelopment), thinning when stands are still young and before the nutrient-rich understory composition has not been dramatically hindered by overstory crown closure is important for providing detectable improvements in winter deer forage availability.

How long do the effects of precommercial thinning last in the understory of young-growth SSWH forests? Further, what does treatment longevity mean? Treatment longevity may refer to the duration that understory vegetation grows faster or is more productive than it was at time zero. This is how some have interpreted the results of Cole et al. (2010) in southeast Alaska, who showed that posttreatment understory cover was greater than pretreatment cover until year 7. Thus, the longevity of treatment for accelerated production was 7 years. A practical alternative definition to longevity is the duration that treated stands have improved understory characteristics over untreated stands. We show, for example, that precommercial thinning results in at least two times more biomass than that of untreated stands (Fig. 3*b*), and after a decade, this effect has not yet shown signs of decreasing. Although Cole et al. (2010) reported pretreatment data, which we do not have in the present study, both of our studies clearly show treatment longevity extending far beyond the temporal scope of these studies (7 and 10 years, respectively) if we contrast understories in thinned stands with those in unthinned stands. Similarly, Alaback (1984) suggests that beneficial effects of thinning on SSWH forest understories may last as long as 20 years. Vegetation dynamics in treated stands have been pushed back because of thinning (Alaback 1984; Oliver and Larson 1996) and now are expected to resume their prior trajectory with at least a 10-year lag — long-term monitoring is needed to determine the point at which these contrasting understories will converge. This practical definition of treatment longevity is important for forest managers trying to forecast vegetation response following active management versus no-action management scenarios because it acknowledges that treatment history has enduring effects on a dynamic system (Deal 2001; Peterson 2002).

These results are relevant to those aiming to diversify maritime forest structure for multiple management objectives. In the Tongass National Forest, the principal land base in southeast Alaska, the United States Department of Agriculture (USDA) Forest Service is poised to transition from old-growth to young-growth timber management over the coming decades (USDA Forest Service 2016). This means that roughly 100 000 ha of existing young growth will likely receive most of the active silviculture in the Tongass into the future, and this study provides valuable insight into management alternatives for those stands. The transition also means that the majority of forested land in the Tongass will be old growth with high deer forage availability (Hanley and Brady 1997) or advancing to an old-growth stage of development. On a landscape level, therefore, future management may be justified to devote fewer resources toward improving wildlife habitat in designated timber stands because of high adjacency (i.e., landscape heterogeneity) between old-growth and young-growth stands. Until then, we demonstrate that precommercial thinning is a useful intermediate treatment to coproduce deer forage and timber in young-growth stands. This particular study only addresses simple silvicultural treatments to stimulate forest understories — it does not address modifications such as differences in residual tree spacing, the use of pruning, or slash management, which are also intended to improve forage availability to deer. Further research is needed to fill these remaining knowledge gaps and further clarify the range of silvicultural prescriptions that can maximize the coproduction of resources. Filling these knowledge gaps across meaningful geographic and operational scales is only possible through the shared stewardship between researchers and managers.

Acknowledgements

This study was made possible by partners with the Tongass National Forest, especially Sheila Spores. TWYGS was initially conceptualized in 2001 in a planning meeting comprised of joint Forest Service Tongass National Forest and Pacific Northwest Research Station personnel: Bob Deal, Gene DeGayner, Tom Hanley, Kim Hastings, Rick Hauver, Patrick Heuer, Rich Jennings, Jerry Jordon, Greg Killinger, Gary Lawton, Larry Meshew, Dave Person, Jim Russell, and Kim Titus. TWYGS was then developed and maintained largely by Michael McClellan, with additional support by David D'Amore and Su Alexander. S. Spores and B. Deal provided insightful reviews of this manuscript.

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