Annelise Z. Rue-Johns[1, 2], **Justin S. Crotteau**[3], **David V. D'Amore**, and **Jeffrey C. Barnard**, USDA Forest Service, Pacific Northwest Research Station, 11175 Auke Lake Way, Juneau, Alaska, 99801

Biomass Regressions for Understory Species in Young-Growth Sitka Spruce–Western Hemlock Forests of Southeast Alaska

Abstract

Quantifying forest understory biomass is important for understanding ecological processes, but there are few methods for non-destructive measurement of understory biomass in southeast Alaska. We developed cover-to-biomass equations for common understory species in young-growth Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) forests. A sampling method of visually estimating cover and destructively measuring biomass was used at 35 stands aged 10 to 67 years on Prince of Wales Island in southeast Alaska from 2007 to 2018. Linear cover to biomass regressions were fitted for 42 species and other genera. In addition to total biomass, regressions were fitted by part (leaves, twigs, wood) for all woody species. Regressions were also fitted for graminoid, fern, forb, shrub, tree, and conifer functional classes. We demonstrate the utility of these regressions by applying them to the Tongass-wide young-growth studies, a rich dataset with understory cover measurements from treated and un-treated stands in four young-growth age classes. Understory biomass was greater in 0- to 5-year-old even-aged stands than stands greater than 15 years old. Treated stands (thinned, etc.) had a greater understory biomass, annual growth, and carbon than untreated stands older than 15 years. Additionally, biomass composition became less woody with increasing stand age in treated stands. These regressions provide an approach to estimate understory biomass, which can be used for evaluation of forest functions, including understory dynamics, wildlife habitats, and total stand carbon.

Keywords: cover-to-biomass regressions, understory dynamics, understory forage, carbon dynamics, Tongass-wide young-growth studies

Introduction

Understory abundance is often used as a metric for gauging forest structure, ecosystem services, and impact of stand management in southeast Alaska (Cole et al. 2010, Hanley et al. 2013, Crotteau et al. 2020b). Canopy cover of understory species is commonly used to estimate abundance because of the simplicity of measurement in the field. However, understory biomass (kg ha^{-1}) often has greater application to ecological functions than canopy cover. Wildlife habitat, for instance, can be evaluated based on the quantification of forage resources using twig and leaf biomass estimates, along with nutritional quality data for each species (Hanley et al. 2012). An additional benefit of biomass estimates is the determination of carbon stocks in understory plants. Thus, while costly to measure directly, estimation of understory biomass is important for understanding forest development, primary production, wildlife forage, carbon storage, and resultant ecosystem services.

Using aerial cover to estimate biomass is common practice in southeast Alaska (see Cole et al. 2010, Hanley et al. 2013, Crotteau et al. 2020b). However, there are no published equations directly linking understory canopy cover to total biomass for woody species or that integrate samples from a breadth of young-growth conditions and ages. Similar cover-to-biomass estimation methods are common in other ecosystems (e.g., Smith and Brand 1983, Muukkonen et al. 2006, MacDonald et al. 2012) and have been found to produce estimates with similar accuracy to other measurement systems (Ónodi et al. 2017). We present regressions for converting understory cover measurements to biomass for 37 common understory species, as

[1]Author to whom correspondence should be addressed. Email: annelise.z.rue-johns@ucdenver.edu
[2]Current address: University of Colorado Denver, Campus Box 171, PO Box 173364, Denver, Colorado 80217
[3]Current address: Rocky Mountain Research Station, 800 E Beckwith Avenue, Missoula, Montana 59801

well as more generally to six functional groups, in young-growth Sitka spruce (*Picea sitchensis* (Bong.) Carrière)–western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests to address the need for improved understory biomass quantification. Additionally, we apply these equations to 8 to 13-year post-treatment data from the Tongass-wide young-growth studies (TWYGS) to illustrate the effects of silvicultural treatment on understory biomass by component. Young-growth stands compose about 295,000 ha of land in southeast Alaska, where they effectively sequester carbon, provide habitat for fauna important to local communities, and grow timber for future regional economies. Nevertheless the enduring ecosystem effects of silvicultural treatment are not known (Crotteau et al. 2020a). Finally, we discuss the application of understory biomass to understory dynamics, deer habitat, and carbon accounting in southeast Alaska.

Methods

Study Area

This study's target population is located in the coastal temperate rainforest of southeast Alaska (Figure 1). Annual precipitation in this region ranges from 160 cm in the northern end of the range to 360 cm in the south, with snowfall varying locally but generally ranging from 90 to 220 cm. Average monthly temperature ranges from 0 °C in January to 13 °C in July. On Prince of Wales Island (lat 55.7, long –132.8), where biomass samples were collected, annual precipitation is approximately 240 cm with 100 cm of snowfall.

Biomass Regressions

Biomass samples were collected over nine field seasons between 2007 and 2018 at 34 study sites representing a range of young-growth age classes, where young-growth refers to naturally regenerated stands that developed following clearcut harvesting. Data were collected in association with the Tongass-wide young-growth studies (TWYGS, further discussed in next subsection) and the Prince of Wales commercial thinning study (POWCT) on Prince of Wales Island (Table 1).

The study sites ranged in age from 10 to 67 years post-harvest at time of sampling. Sites were located in Sitka spruce–western hemlock stands (Viereck et al. 1992) and contained a combination of untreated stands and managed stands treated with alder planting, thinning, and thinning in combination with pruning or slash management, depending on age class. Samples were collected from mid-June to mid-August, and each site was sampled in up to three seasons. Alaback (1986) found that understory cover and biomass, as measured by visual estimates and destructive sampling, do not change significantly over this seasonal time period in the study area.

For each understory species, crews visually estimated percent cover to the nearest 1% and destructively sampled all above-ground vascular plant biomass within sample quadrats (Hanley et al. 2012). The understory was defined as all vascular plants except trees with a diameter greater than 2.5 cm at breast height (1.37 m). Only vegetation under 1.37 m was included in measurements because it was a convenient empirical threshold between understory and mid to overstory vegetation. Only two species, *Oplopanax horridus* and *Sambucus racemosa*, exceeded this height in the field. Crews then separated each woody species into leaves, twigs, and wood and weighed each in the field to the nearest gram (> 100 g) or tenth gram (≤ 100 g) with Pesola spring scales (Pesola, Schindellegi, Switzerland). Twigs were defined as stems from the current growing season. For conifers, needles and twigs were weighed together. Ferns, forbs, and grasses were not separated by part. In some cases, a representative subsample was weighed by part to facilitate faster sample processing. After measuring field weight, a subsample of each species part was oven-dried at 100 °C to a stable weight. Wet-to-dry proportions were calculated daily for each species part and used as conversion factors to calculate dry biomass for each sample taken in the field. In the 2007 to 2008 TWYGS and 2014 POWCT seasons, a double-sampling method was used in which 1 m^2 quadrats (0.67 m^2 in 2014) were placed systematically and all species present were measured. In all other years, targeted samples of the most common understory species were collected to fill a range of 10% cover

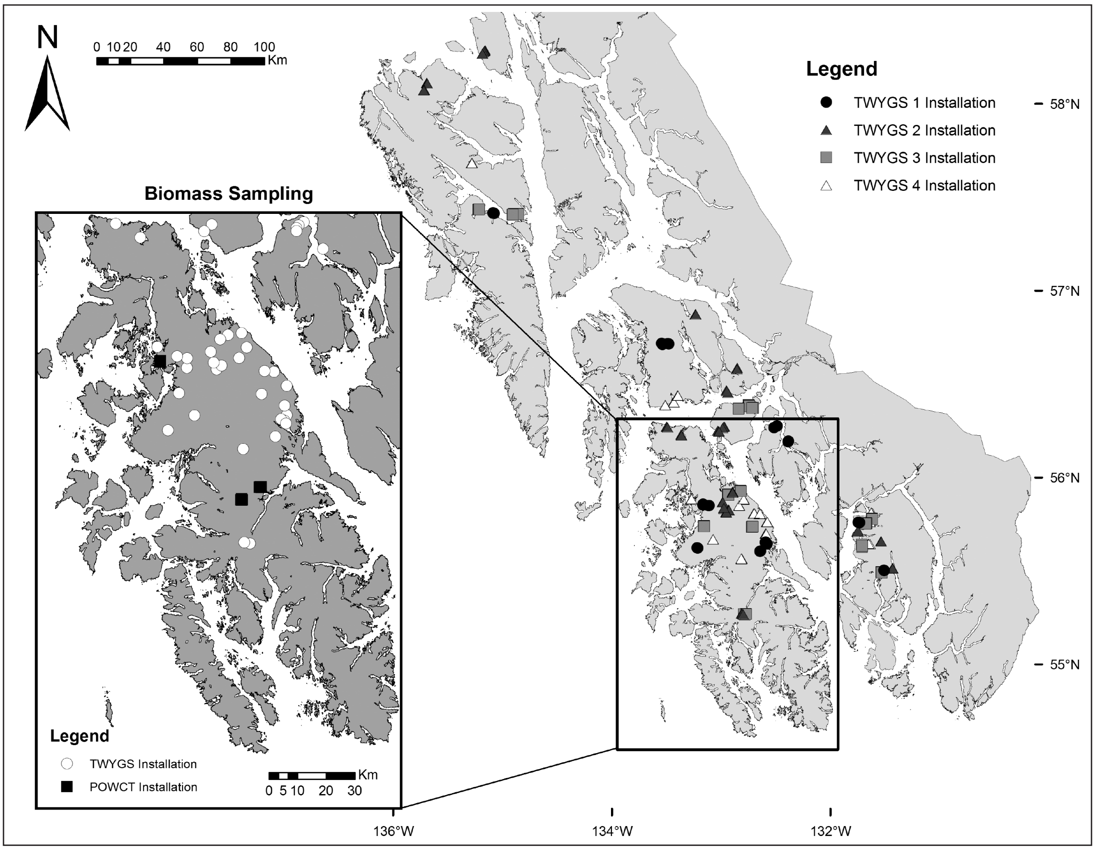

Figure 1. Map of Tongass-wide young-growth studies (TWYGS) and Prince of Wales commercial thinning (POWCT) experimental sites. All units contain both control and treated units (see Table 1 for treatment descriptions). Biomass sampling was conducted at all TWYGS and POWCT sites on Prince of Wales Island (inset), while the TWYGS experiment has sites throughout southeast Alaska.

increments (0 to 10%, 10 to 20%, etc.) of each species. Quadrats used for targeted sampling were 1 m^2, 0.25 m^2, or 0.10 m^2 depending on species growth pattern.

Linear cover-to-biomass regressions were developed in R (R Core Team 2018) for each species with more than six samples. All regressions were fit to the form $\ln(B) = \beta_0 + \beta_1 \times \ln(C)$, where B is oven-dry biomass (kg ha^{-1}), C is areal cover (%), and β_0 and β_1 are the estimated regression coefficients. Residuals from each species model were examined for normality using Q-Q plots, and logarithmic transformations were used to account for heteroscedasticity. For simplified biomass prediction, this form can be rewritten as $B = e^{\beta 0} \times C^{\beta 1}$. Regressions were also calculated for each plant part (leaves, twigs, wood) using the same method. For species or genera that had less than 5% cover in all measurements, the mean dry biomass value is presented in place of a regression. To better estimate biomass for uncommon species, general regressions were also developed by fitting regressions of the same form to all plants in six functional classes: graminoids, ferns, forbs, shrubs, conifers, and other trees. Along with coefficients for use in biomass prediction, we report coefficient standard errors, absolute and normalized root mean square error (RMSE and NRMSE), and R^2 for users to better understand model fit accuracy and variability.

TABLE 1. Description of Tongass-wide young-growth studies (TWYGS) and Prince of Wales commercial thinning (POWCT) experiments, all of which include untreated controls. Biomass samples were collected from all experimental units on Prince of Wales Island (Figure 1). The regressions were applied to data from the four TWYGS experiments.

Experiment	Age when treated	Treatment type	Number of biomass sampling units	Number of TWYGS units
TWYGS 1	0 to 5	Alder planting	9	17
TWYGS 2	15 to 25	Precommercial thinning	8	18
TWYGS 3	25 to 35	Precommercial thinning and pruning	6	13
TWYGS 4	35+	Precommercial thinning and slash treatment	8	17
POWCT	49 to 62	Commercial thinning	3	N/A

Assessment of Treatment Effects on Understory Biomass

The Tongass-wide young-growth studies (TWYGS) are comprised of four silvicultural experiments to improve timber and forage, each including both control units and treatments applied to a different age class of stands across southeast Alaska between 2002 and 2006 (Table 1). In the first and youngest experiment ("TWYGS 1", treated 0 to 5 years post-harvest), red alder (*Alnus rubra* Bong.) was planted to increase structural diversity and enrich conifer regeneration in 17 stands, with planting densities of 334 and 549 trees per hectare (tph). In the second experiment ("TWYGS 2", treated 15 to 25 years post-harvest), pre-commercial thinning with leave densities of 334 and 549 tph were applied to 18 stands. In the third experiment ("TWYGS 3", treated 25 to 35 years post-harvest), pre-commercial thinning with a leave density of 420 tph was applied to 13 stands in addition to pruning 0%, 25%, or 50% of conifers to a height of 2.7 or 5.2 m. In the fourth experiment ("TWYGS 4", treated 35+ years post-harvest), 17 stands were pre-commercially thinned to a leave density of 198 tph, either by girdling or felling with no slash treatment, slash bucking to 1.5 m, or slash bucking to 4.6 m. Each experiment included active treatment units and untreated controls. For a complete discussion of the TWYGS treatments and methods, see Hanley et al. (2013) and Crotteau et al. (2020a).

For demonstration in this study, we decided to showcase the second complete measurement cycle for the suite of TWYGS experiments (8 to 13 years post-treatment), which took place between 2012 and 2016. Here, understory cover was measured in 60 1-m^2 quadrats in each experimental unit. The regressions developed in the current study, which pooled treatments and measurement cycles, were applied to each species, and total biomass per unit was calculated. Additionally, the current annual growth (leaves and twigs) and the proportion of total biomass from wood was calculated for each unit. Finally, total understory carbon was estimated by multiplying the total biomass by 0.48 (Lamlon and Savidge 2003) to allow comparison with other carbon pools in the region. We tested for experiment (TWYGS 1, 2, 3, or 4) and treatment (pooled treated or untreated) effects on total stand understory biomass using an Analysis of Variance test and quantified the difference in group means by Tukey-Kramer's post-hoc tests using the R's agricolae package (Mendiburu 2019). We examined residuals for normality and variance homogeneity. The same analysis was completed using current annual growth, the proportion of total biomass from wood, and understory carbon as response variables.

Results

Biomass Regressions

Of the 35 species and seven genera that had six or more samples, 34 species and three genera had cover distributions acceptable for regression analysis (i.e., at least 10% cover; Table 2). Each regression included between 13 and 987 samples, with R^2 ranging from 0.20 to 0.95. Each functional class grouping included between 76 and 2,733

TABLE 2. Cover-to-biomass regressions for total biomass (kg ha^{-1}) of common understory species and functional classes in the form ln(Biomass) = $\beta_0 + \beta_1 \times$ ln(Cover). Nomenclature follows the USDA PLANTS database (USDA, NCRS 2019). NRMSE was calculated as RMSE divided by the standard deviation of Biomass in each species. Cover range (%) indicates the range of the independent variable used to fit the regressions. For biomass regressions fitted by part, see Supplemental Table S1 (available online). Note that the standard errors of the β_0 and β_1 coefficients are for ln(Biomass), not Biomass directly.

Species	Number of samples (n)	β_0 (SE)	β_1 (SE)	RMSE	NRMSE	R^2	Cover range (%)
Graminoids							
General graminoids	223	–0.472 (0.081)	1.080 (0.046)	1.13	0.08	0.71	0–100
Carex spp.	18	–0.125 (0.389)	0.489 (0.242)	1.36	0.19	0.20	0–50
Luzula spp.	20	–0.804 (0.280)	1.525 (0.166)	1.11	0.26	0.82	0–10
Ferns							
General ferns	2,733	–1.274 (0.029)	1.165 (0.011)	1.01	0.03	0.80	0–100
Athyrium filix-femina	471	0.030 (0.083)	1.258 (0.030)	1.11	0.02	0.79	0–100
Blechnum spicant	391	0.025 (0.065)	1.100 (0.025)	1.02	0.02	0.83	0–100
Dryopteris expansa	947	–1.332 (0.047)	1.156 (0.020)	0.99	0.05	0.78	0–100
Gymnocarpium dryopteris	733	–1.328 (0.054)	1.124 (0.021)	0.85	0.05	0.80	0–100
Phegopteris connectilis	131	–1.349 (0.189)	1.232 (0.054)	0.87	0.02	0.80	0–100
Polystichum braunii	23	–0.566 (0.257)	1.292 (0.088)	0.81	0.00	0.91	0–100
Pteridium aquilinum	21	0.166 (0.460)	1.092 (0.121)	0.47	0.01	0.81	0–100
Forbs and subshrubs							
General ferns and subshrubs	1,951	–0.831 (0.030)	1.021 (0.012)	1.05	0.03	0.79	0–100
Chamerion angustifolium	28	–0.612 (0.295)	1.458 (0.098)	1.08	0.01	0.90	0–100
Circaea alpina	96	–1.796 (0.135)	1.090 (0.052)	0.96	0.11	0.83	0–100
Coptis aspleniifolia	180	–0.841 (0.094)	1.027 (0.035)	1.01	0.06	0.83	0–100
Cornus canadensis	466	–0.512 (0.059)	0.974 (0.024)	0.91	0.05	0.78	0–100
Galium spp.	24	–1.688 (0.187)	1.112 (0.124)	0.78	0.25	0.77	0–25
Linnaea borealis	15	0.637 (0.287)	0.852 (0.251)	1.03	0.29	0.47	0–10
Lysichiton americanus	152	–1.040 (0.228)	1.240 (0.065)	1.00	0.01	0.71	0–100
Maianthemum dilatatum	49	–1.243 (0.161)	1.048 (0.093)	1.06	0.16	0.73	0–75
Nephrophyllidium crista-galli	18	0.332 (0.434)	0.958 (0.117)	0.38	0.01	0.81	0–100
Rubus pedatus	317	–0.530 (0.065)	0.882 (0.029)	1.02	0.10	0.74	0–100
Tiarella trifoliata	509	–0.994 (0.053)	0.953 (0.020)	0.90	0.09	0.81	0–100
Shrubs							
General shrubs	2,181	–0.096 (0.047)	1.266 (0.016)	1.34	0.01	0.75	0–100
Gaultheria shallon	18	1.588 (0.382)	0.934 (0.104)	0.31	0.00	0.83	0–100
Menziesia ferruginea	361	–0.050 (0.122)	1.261 (0.042)	1.41	0.01	0.72	0–100
Oplopanax horridus	141	–0.020 (0.290)	1.243 (0.077)	0.99	0.00	0.65	0–100
Ribes bracteosum	121	–0.002 (0.189)	1.161 (0.060)	1.13	0.01	0.77	0–100
Ribes lacustre	29	–0.002 (0.432)	1.161 (0.116)	0.69	0.00	0.77	0–100
Ribes laxiflorum	38	0.672 (0.496)	1.099 (0.131)	0.70	0.01	0.77	0–100
Ribes spp. (other)	13	–0.529 (0.440)	1.166 (0.255)	1.37	0.06	0.66	0–40
Rubus parviflorus	14	–1.402 (0.259)	1.453 (0.079)	0.32	0.00	0.95	0–100
Rubus spectabilis	564	–0.530 (0.086)	0.882 (0.030)	1.21	0.01	0.78	0–100
Sambucus racemosa	114	–0.802 (0.191)	1.303 (0.054)	0.73	0.01	0.85	0–100
Vaccinium ovalifolium [1]	681	0.165 (0.079)	1.315 (0.028)	1.47	0.01	0.76	0–100
Vaccinium parvifolium	70	1.318 (0.283)	1.140 (0.087)	0.99	0.00	0.72	0–100

TABLE 2. *Continued*

Species	Number of samples (*n*)	β_0 (SE)	β_1 (SE)	RMSE	NRMSE	R^2	Cover range (%)
Trees (understory)							
General conifers	1,940	0.369 (0.029)	1.253 (0.015)	1.23	0.00	0.80	0–100
General non-conifers	76	–0.200 (0.224)	1.357 (0.076)	1.04	0.00	0.82	0–100
Alnus rubra [2]	63	–0.232 (0.206)	1.276 (0.074)	0.94	0.01	0.84	0–100
Callitropsis nootkatensis	18	1.812 (0.406)	1.188 (0.124)	0.73	0.00	0.85	0–100
Picea sitchensis	829	0.452 (0.045)	1.268 (0.025)	1.19	0.01	0.78	0–100
Pinus contorta var. *contorta*	22	2.512 (0.616)	1.028 (0.161)	0.56	0.00	0.67	0–100
Thuja plicata	84	0.776 (0.153)	1.364 (0.051)	1.00	0.00	0.90	0–100
Tsuga heterophylla	987	0.238 (0.040)	1.174 (0.020)	1.22	0.01	0.77	0–100

[1]*V. ovalifolium* regressions include both *V. ovalifolium* and *V. alaskense* due to experimental protocol; these species are difficult to differentiate in the field and follow identical growth patterns.
[2]Data collected in association with the TWYGS 1 experiment were excluded from fitting *A. rubra* regressions due to the experimental design (alder planting).

samples, with regression R^2 ranging from 0.71 to 0.80 (Table 2). Regressions for leaves, twigs, and wood were fit for 13 shrub and non-conifer tree taxa (Supplemental Table S1, available online only). Model R^2 for regressions ranged from 0.41 to 0.87 for leaves, 0.08 to 0.90 for twigs, and 0.41 to 0.81 for wood. Of the four species and genera with less than 10% cover (Table 3), the number of samples ranged from 10 to 36.

Assessment of Treatment Effects on Understory Biomass

Total understory biomass was significantly affected by TWYGS experiment (TWYGS 1, 2, 3, or 4), treatment (control or treated), and their interaction (Table 4). Total biomass was greatest in TWYGS 1 stands and was not significantly affected by the alder planting treatment (Table 5). Treated units in TWYGS 2, 3, and 4 had similar understory biomass, which was greater than that of untreated stands in the same experiments. Current annual growth was significantly affected by experiment ($P < 0.001$), treatment ($P < 0.001$), and their interaction ($P < 0.001$), and patterns were similar to those of total biomass. Understory carbon patterns were identical to total understory biomass.

Regardless of treatment, the proportion of biomass made up of wood decreased with stand age, with the exception of treated stands in the 25 to 35 year age class (Table 5). Proportion of biomass from wood was significantly affected by experiment ($P < 0.001$) and treatment ($P = 0.02$) (Table 4). Wood composed 77.2% of total biomass in TWYGS 1 untreated stands, while making up only 47.7% of total biomass in TWYGS 4 untreated stands. In both treated and untreated units, the proportion of biomass from wood was significantly higher in TWYGS 1 units than TWYGS 4 units, with TWYGS 2 and 3 intermediate in untreated stands.

Discussion

Comparison to Other Methods of Understory Biomass Estimation

Assessment of understory biomass is broadly important to ecological sciences, so acquiring appropriate species-specific estimates is essential. There are multiple approaches to measuring understory biomass, including both destructive and non-destructive methods. Destructive methods are generally more accurate than non-destructive methods but also more expensive. Non-destructive methods are often preferred for long-term studies, as indirect biomass measurements can be taken without affecting future growth. Regression equations are a simple way to estimate biomass using non-destructive measurements.

TABLE 3. Mean biomass for species with cover ranges less than 5%. Nomenclature follows the USDA PLANTS database (USDA, NCRS 2019). Cover range (%) indicates the cover values of samples used to calculate the means.

Species	Mean biomass (kg m^{-2})	Number of samples	Cover range (%)
Equisetum spp.	0.0012	10	0-4
Moneses uniflora	0.0006	36	0-5
Streptopus spp.	0.0002	14	0-2
Viola spp.	0.0006	19	0-5

Previous regression equations for understory biomass in southeast Alaska have used a variety of non-destructive measurements, only some of which included areal cover (Hanley et al. 2013, Alaback 1986). Yarie and Meads (1989) developed a collection of allometric regressions that estimated biomass from cover for defined height segments. Their methodology included stacking square meter quadrats vertically at 10-cm intervals and estimating the areal cover of each species in each interval. This approach made fewer assumptions about plant height than a simple cover-to-biomass method, but the measurement process was costly. While the inclusion of vegetation height could improve the precision of our estimates, some studies have found that height measurements do not improve model fits (e.g., Huff et al. 2017). Alaback (1986) found that factors other than cover estimates may be stronger predictors of understory biomass for some species. In many shrubs, for instance, stem diameter and length were a better predictor of woody biomass than areal cover. Such allometries may be more accurate than using cover to predict biomass, but they are more difficult and time consuming, which precludes extensive understory measurement. Furthermore, predictive equations using multiple (e.g., cover plus height) or more expensive (e.g., stem length) measurements are not easily crosswalked for widespread use on many existing datasets.

An alternative approach to estimating understory biomass from cover is to include only current annual growth, as in regressions previously reported in association with the TWYGS experiments (Hanley et al. 2013). While this method may be effective for some applications, such as wildlife habitat, it excludes the 48 to 87% of total understory biomass from wood in young growth stands (Table 5), which is essential for accurately assessing stand carbon and understory structure. Additionally, understory biomass estimates that include woody biomass are directly comparable to other reports of biomass and carbon.

Hanley et al. (2013) reported regression coefficients for major understory species in this forest type, but they were fitted by measurement year and omitted woody biomass. By using that approach, researchers indirectly incorporated annual climatic conditions into their analysis of TWYGS biomass. Crotteau et al. (2020b) found that growing season temperature and precipitation affect understory biomass, suggesting that understory comparison across years may be confounded by climatic variation. Pooling of understory biomass data across measurement years may result in loss of this annual variation in growing conditions, and thus limit visibility of interesting vegetation dynamics. However, by using an extended sampling time scale, our biomass regressions are more broadly applicable to other annual growing seasons.

Application of Understory Biomass Estimates

Knowledge of understory biomass in southeast Alaska's forested ecosystems has broad implications for understanding understory composition, wildlife habitat, and carbon sequestration. Informed management of these ecosystem characteristics and services, whether in the form of silvicultural treatments or forest plan development, depends on accurate assessments of understory biomass.

Understory Dynamics—Understory responses to overstory structure and light are quantified by plant composition and production (i.e., biomass), which change with stand age (Alaback 1982), overstory composition (Deal et al. 2004), and silvicultural treatment (Hanley et al. 2013, Crotteau et al. 2020b). Framing the TWYGS experiments as a chronosequence, we found that understory biomass was greatest in the 0- to 5-year age class and reduced in both unthinned and thinned stands after 15 to 25 years, consistent with a decrease in

TABLE 4. Linear models of experiment and treatment effects on understory biomass in Tongass-wide young-growth studies (TWYGS) experiments. Experiment (TWYGS 1, 2, 3, or 4), treatment (treated or untreated control), and their interaction significantly affect total understory biomass and current annual growth (leaves and twigs), while experiment and treatment significantly affected proportion of biomass from wood.

		Total biomass		Current annual growth		Proportion of wood	
Factor	Degrees of freedom	*F*	*P*	*F*	*P*	*F*	*P*
Experiment	3	55.02	< 0.001	30.74	< 0.001	18.97	< 0.001
Treatment	1	39.48	< 0.001	54.54	< 0.001	5.53	0.02
Interaction (E × T)	3	4.84	0.003	5.50	0.001	1.85	0.13
Residuals	232	-	-	-	-	-	-

TABLE 5. Understory response in treated and untreated units of four Tongass-wide young-growth studies (TWYGS) experiments. Treatments were implemented 8 to 13 years before measurement. Active treatments were pooled together by experiment for this study (e.g., "Alder planting" refers to pooled 334 and 549 trees ha^{-1} planting densities). Mean values reported with standard error (SE) in parentheses. Letters denote Tukey-Kramer pairwise tests within each column; same letters indicate no significant difference.

TWYGS experiment (age when treated)	Treatment	Total understory biomass (kg ha^{-1})	Current annual growth (kg ha^{-1})	Proportion understory woody biomass (%)	Carbon (kg ha^{-1})
1 (0 to 5)	Control	2,660.4 (288.4) a	792.2 (76.4) ab	77.2 (2.4) ab	1,277.0 (138.4) a
1 (0 to 5)	Alder planting	2,619.9 (177.8) a	829.1 (57.0) ab	76.6 (1.7) ab	1257.5 (85.4) a
2 (15 to 25)	Control	387.5 (98.7) c	156.5 (39.8) e	70.0 (6.4) bc	168.0 (47.4) c
2 (15 to 25)	Thinning	1,242.5 (126.4) b	427.3 (32.8) d	71.4 (3.2) bc	596.4 (60.7) b
3 (25 to 35)	Control	200.7 (77.0) c	81.0 (27.9) e	68.4 (11.3) bcd	96.4 (36.9) c
3 (25 to 35)	Thinning + pruning	1,236.3 (141.1) b	508.4 (53.7) cd	86.7 (3.7) a	593.4 (67.7) b
4 (35+)	Control	311.3 (88.9) c	177.9 (49.4) e	47.7 (6.4) d	149.4 (42.7) c
4 (35+)	Thinning + slash treatment	1,343.6 (84.8) b	629.0 (35.8) bc	58.7 (2.2) cd	646.0 (40.7) b

understory light following canopy closure. This corresponds to a trend of increasing understory biomass in young stands until canopy closure approximately 20 years after harvest (Alaback 1982). Additionally, decreases in light with age and canopy closure had a substantial impact on the type of understory biomass (i.e., woody versus non-woody) present in young-growth stands (Table 5). When closed canopies were re-opened by thinning, understory biomass and production increased by 10 years after treatment, but the distribution of biomass among understory components (woody versus non-woody) remained static and never attained the pre-canopy closure state (i.e., represented by the 0- to 5-year age class), suggesting a notable shift in understory dynamics because of time of treatment. This may indicate changes in functional class composition associated with stand age, such as an increase in the proportion of ferns in older stands, which have been identified in other studies of young-growth stands in this region (e.g., Alaback 1982, Hanley et al. 2013, Crotteau et al. 2020b). Accurate assessment of understory biomass is essential for evaluating the successional trajectories of managed and unmanaged stands under varying light conditions.

Deer Forage—Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) is a common ungulate and valuable game species in southeast Alaska that depends on understory vegetation for forage (Hanley et al. 1989). Biomass can be used in association with nutritional quality of plant parts to predict the nutritional resources of given understory forage. A food-based estimate of the maximum population supportable by the predicted nutritional resources can then be made using established ungulate nutrient requirements. The forage resource evaluation system for habitat (FRESH-Deer) model calculates the maximum supportable population based on digestible energy and digestible protein derived from understory biomass (Hanley et al. 2012, 2013).

Quantification of available forage using FRESH-Deer requires the calculation of understory biomass for each species and plant part (leaves, twigs, and wood) to account for differences in nutritional composition (Hanley et al. 2012). Stands with similar total understory biomass may contain different available forage if their composition differs in nutritional quality, so species-specific biomass regressions are essential. Thus, the regressions presented in this study provide a necessary component for assessment of deer forage availability from measurements of understory cover.

Carbon—The calculation of total stand carbon can be completed with much more confidence given our new equations for understory biomass. Total stand carbon is not greatly increased with the addition of understory carbon to overstory carbon, but patterns of carbon allocation during stand development have implications for overall stand nutrient cycles and future patterns of carbon sequestration. Stand thinning treatments that are implemented to improve deer forage stocks, such as those used in the TWYGS experiments, initially reduce carbon stocks due to loss of standing biomass (D'Amore et al. 2015). The increase in the woody carbon component in this case mitigates the loss of carbon by 0.3 to 3.1% across thinning intensity and can be used to update estimates of the overall reduction in carbon stocks after thinning treatments. Tree carbon is much higher than understory carbon across the stand types and treatments, as values for tree carbon in young growth stands is about 398 Mg ha^{-1} (D'Amore et al. 2015) compared to about 0.6 Mg ha^{-1} for understory (Table 5).

Woody tissue of understory plants accounted for the majority of the biomass across all treatments and sites. However, greater total woody biomass in younger TWYGS treatments compared to older treatments reveals a shift in carbon allocation in stands across time. This stem component of the understory plants is more persistent and provides a small, but potentially more stable, component of ecosystem carbon than foliage over time. The accumulation of understory woody biomass and associated root growth likely stimulates soil organic matter turnover and enhances nutrient availability compared to closed-canopy conditions in later stand development (Kuzyakov 2002). The woody accumulation may shift back to a more readily available nutrient pool for trees as the shrub stems decompose in the near surface. Finally, abundant woody stems can produce copious amounts of annual foliage, which may be an important source of priming for overall stand productivity.

Conclusion

The biomass regression equations that we present in this study have wide utility, and can help strengthen inference on a number of studies that report understory cover measurements. There is some evidence that the regression coefficients for a small number of species may vary across stand conditions, such as disturbance history, available light, or overstory composition (Alaback 1986, Yarie and Mead 1989). However, further sampling across stand conditions is necessary to quantify those effects. The equations presented here are most applicable to young-growth stands on Prince of Wales Island, but should be useful across the wide range of Sitka spruce–western hemlock forests in the Pacific Northwest.

Biomass of understory components are valuable metrics for assessing forest structure and function. Estimating biomass quickly, accurately, and non-destructively is important for a wide variety of ecological studies. These equations provide a simple and repeatable way for forest managers, practitioners, and scientists to more effectively quantify the array of services that forest understories provide.

We applied these equations to the Tongass-wide young-growth studies and demonstrated three key findings: 1) understory biomass is increased by pre-commercial thinning; 2) understory biomass decreases with stand age; and furthermore, 3) the proportion of woody biomass in the understory decreases with stand age. These findings demonstrate the utility of this study's equations and highlight important nuances regarding wildlife habitat, carbon, and stand dynamics in southeast Alaska.

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