

Biomass Regression Equations for Understory Plants in Coastal Alaska: Effects of Species and Sampling Design on Estimates

Abstract

Biomass prediction equations were developed for 9 species of shrubs and trees and 16 species of herbs and bryophytes from 24 coastal sampling sites in southeastern Alaska. Samples were taken from clearcuts and from second-growth and old-growth forests. Stem diameter was the best predictor of shrub biomass. For all herbs, except some ferns and members of the Liliaceae, percentage of ground cover was the best predictor. Regression equations accounted for 74 to 99 percent of biomass variation, and differences between slopes of most equations for different species were highly significant. Slopes and y-intercepts were generally related to vegetation sere or autecology of the species. Species with monolayer canopies generally accumulated less biomass per stem or ground area than species with multilayered canopies. Date of sample collection (1 July to 1 Sept.) was not related to biomass. From 10 to 15 4-m² plots or 30 to 60 1-m² plots, systematically placed, were needed for precise estimates of understory biomass in mature or old-growth forests. In recently disturbed vegetation, more than 15 4-m² or 60 1-m² plots were needed for precise estimates. Plots 4-m square were more efficient than plots 1-m or 0.1-m square for estimating biomass to a given level of precision.

Introduction

Despite widespread use of regression equations for biomass estimates, the variation among species in plant dimension-biomass relationships has been little examined. If patterns in this relationship can be related to the general morphology or autecology of different species, equations selected for biomass estimates will be more appropriate, more field efficient, and less biased.

Most emphasis has been placed on large, dominant, woody species in which much of the forest biomass is accumulated, yet such species may not characterize ecosystem dynamics as well as understory vegetation (< 2 m tall), which responds to subtle changes in stand structure, microclimate, and edaphic factors (e.g., Anderson *et al.* 1969). Information on understory productivity may be critical for understanding processes such as nutrient cycling and animal foraging. Also, large-scale destructive sampling of vegetation biomass is more practical for the understory than overstory. These factors make desirable an investigation of the relationship of plant genetics and environment to plant dimensions and biomass.

Parameter coefficients for individual species and, in some cases, for particular growing sites may vary widely, as relationships between plant

biomass and size class are empirically derived (Agee 1983). For unbiased biomass estimates, relationships of biomass and plant dimensions should be developed for each species common to a given habitat type or productivity class. Biomass regression equations are often used interchangeably among species with little theoretical basis, and some understory strata are wholly ignored.

This study examines biomass and—where practical—productivity of shrubs, herbs, ferns, mosses, liverworts, and lichens that are widespread in the Pacific Northwest, Canada, and southern Alaska. Objectives were: 1) to determine easily measured variables that best relate to biomass and productivity of understory vegetation in coastal Alaska, 2) to develop equations for the relationships of plant size-class to biomass of each species, and 3) to characterize the variability of biomass equations in differing environments and with differing methodologies.

Methods

Site Selection

The 24 sites for destructive sampling were selected for a range of environments within the *Picea sitchensis-Tsuga heterophylla* (Sitka spruce-western hemlock) forests of southeast Alaska (Table 1); for homogeneity of vegetation, slope, and aspect, and for ease of access. Each was below 150 m elevation on well-drained gentle

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slopes (< 20 percent) and included closed-canopy (> 70 percent mean canopy cover) or clearcut forests. Most sites had been previously sampled for studies of secondary succession and overstory-understory relationships (Alaback 1982a, 1982b).

Biomass samples were taken over a 2-month period rather than for the estimated period of "peak understory biomass" because of the short Alaskan summer and the distance between sites, more than 400 kilometers (Grigal *et al.* 1976). One site was sampled on 29 June, 29 July, and 28 August in order to test whether the time scheme biased estimates of plant biomass. Development of a relative index of the date of sample collection within the growing season of a site further identified the effect of phenology on biomass estimation. The relationship of growing season to latitude was developed from available meteorological data (National Oceanographic and Atmospheric Administration 1978). Time and length of the growing season was then estimated for each study site.

Species Selection

Relative abundance of each understory vegetation species was estimated on 60 sites over a broad range of stand age-classes, geographic locations, and edaphic conditions (Alaback 1982b). Seventy-eight species were found. More than 70 percent of the ground cover was occupied by the 10 most abundant species. Aboveground biomass of all vascular plant species averaging more than 0.1-percent ground cover (relative to other vegetation rather than to total land area) was sampled—seven woody shrub species, nineteen herbaceous or low-growing shrub species, and the nine most abundant bryophyte and lichen species.

Sampling Procedure

From low-growing shrubs such as *Cornus canadensis* (bunchberry) and *Rubus pedatus* (trailing bramble), only vertical shoots (not rhizomes or runners) were sampled. Woody-shrub shoots were cut flush with the forest litter layer. Woody shrub shoot height, basal diameter, and vigor class were tested for their relationship to biomass. Vigor was defined as the percentage of live twigs and branches per individual shrub canopy. Primary productivity of deciduous herbs was assumed to be equal to aboveground biomass, and that of

shrubs was measured as the biomass of current annual twigs and deciduous foliage. Foliar production of evergreen species, which normally retain leaves for three years, was assumed to be one-third that of the foliar biomass. Moss samples, clipped at ground level, did not include decomposing, nonyellow or nongreen parts.

Specimens were collected between 1 July and 1 September, 1977 to 1984. During the first year, emerging stems of all plants rooted within 1-m² quadrats randomly located throughout several study sites were measured and collected for drying, a scheme that resulted in oversampling of the most abundant species. Subsequently, species and size-classes on each site were determined first, then each was randomly sampled for a more equitable distribution.

First, selected specimens were measured non-destructively, then samples were collected and components separated into paper bags for drying and weighing. Some samples were taken intact into the laboratory for more efficient separation. All were dried at least 24 hours at 70°C, then stored in plastic bags to retard absorption of ambient humidity. Weight was recorded to the nearest 0.001 g on specimens of less than 10 g and to the nearest 0.1 g on those greater than 10 g.

All plants in each 1-m² or 4-m² plot in each of the 60 previously studied sites (Alaback 1982a, 1982b) were measured preparatory to determining the effects of sampling intensity on understory biomass estimates. A random-number generator selected successively increasing numbers of plots for the estimates in each stand. Four runs with four sets of randomly chosen plots were made for each stand in order to characterize variability with increasing sampling intensity. Sampling-area curves, a simple extension of the concept of a species area curve (Cain 1938), were then plotted for each of the 60 sites. Sample variance and number of plots necessary for estimates within 10 percent of the mean were calculated for all sites (Cochran 1963).

Parameter Selection

Biomass-equation parameters were selected for precision of prediction and maximum field efficiency. If plant densities varied widely, more than one set of independent variables was used for each species. Parameters for biomass estimation were initially chosen for dense stands of

western hemlock (*Tsuga heterophylla*) that often have a sparse understory, especially in seral stands (Alaback 1982a). When more dense vegetation was sampled, more expeditious but often less precise estimation techniques were developed. *Gymnocarpium dryopteris* (oak fern) and *Streptopus roseus* (twisted stalk) are two species that required more than one sampling strategy. In depauperate stands, all fronds or shoot lengths in a 1-m² plot were measured; in open, mesic forests, where these species often formed dense thickets, the relation of the percentage of ground cover to biomass was used in the regression model. The few biomass studies that have included bryophytes have employed core sampling or area-based destructive sampling rather than dimension analysis (Forman 1969, Clymo 1970). Dimension analysis was used here for maximum field efficiency and for compatibility with data collection for other species.

Statistical Analysis

Regression equations were developed by means of the SPSS statistical subroutines on the CDC CYBER computer at Oregon State University and the MICROSTAT software on an 8-bit microcomputer. For most species, two models gave the best results: the log-log transformation or the simple (untransformed) linear model (Draper and Smith 1966). Since equations applied to depauperate vegetation often predict negative biomass at the low extreme of independent variables (i.e., percentage of ground cover < 5 percent), separate equations were developed for the low range when they improved accuracy. Final equations were adjusted for logarithmic bias (Baskerville 1972).

Comparisons of regression equations were made by calculating F statistics from a full-parameter regression model and a series of reduced models. In the full model, the slopes and y-intercepts of all regression equations were included; in reduced models, only those for regression equations of a species subset were included. If significant differences were detected, pairwise comparisons were made of individual equations by changing the design matrix to include only those equations (Neter and Wasserman 1974).

Results

Percentage of ground cover was linearly related to the biomass of most species. Only species with

substantial height variation showed a curvilinear relationship (Tables 2, 3). Virtually all regressions based on stem diameter or shoot length were curvilinear, a pattern in general agreement with other dimension analyses of shrubs and trees (Brown 1976, Gholz *et al.* 1979, Stanek and State 1978, Smith and Brand 1983). At the low extreme of ground-cover area (0-10 percent), biomass also had a curvilinear relationship. This change in equation form with low cover may relate to changes in plant morphology with age and size, factors less important when the plants are mature and occupy more area.

Effects of Species

Woody species. Because of the vertical dimension and variable structure of woody shrub species, measures of abundance such as percentage of ground cover or frequency of occurrence are usually imprecisely related to biomass (Table 4). Overall, the amount of shrub cover bore a good relationship to biomass; however, the same amount corresponded to drastically different biomass density in clearcuts and old-growth (Figure 1). A cover-based biomass regression equation is not a good general-purpose equation for a range of site conditions, as it will give highly imprecise estimates. Twenty-three to eighty percent of the variation in shrub biomass was accounted for by the percentage of cover measured on 22 sites in 1978. The mean square error (MSE) of biomass estimates was 1.5 to 15 times greater with regression equations based on percentage of cover than with those based on stem diameter (Tables 2, 3). Plot size also made a substantial difference. Large, clumped species such as *Menziesia ferruginea* (rusty menziesia) had a significant relationship to biomass on 4-m² plots but an insignificant one on smaller plots ($P = 0.05$).

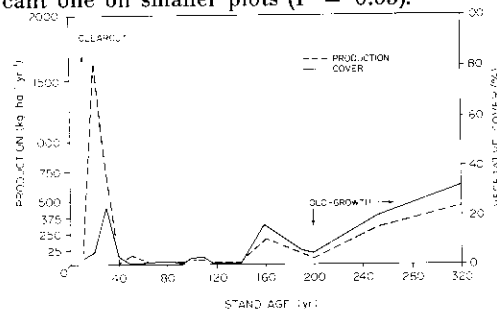


Figure 1. Relation of productivity of *Vaccinium alaskaense* to percentage of ground cover over a chronosequence of stands (Alaback in press).

TABLE 1. Characteristics of 24 sites selected for destructive biomass sampling in southeast Alaska.¹

Location	Age Class ²	Site Index (m•100 yr ⁻¹)	Elevation (m)	Stand Origin
Clark Bay	Clearcut	--	38	Logging
Douglas Bay	Clearcut	36	5	Logging
Harris River ³	Clearcut	38	67	Logging
Maybeso Valley	Clearcut	40	91	Logging
Thomas Bay	Clearcut	31	8	Logging
Tuxekan Island	Clearcut	30	30	Logging
Agate Beach	Mature	31	7	Logging
Bartlett Hospital	Mature	37	30	Windthrow
Edna Bay	Mature	40	30	Logging
Kanulku Bay	Mature	32	30	Fire
Kindergarten Bay	Mature	30	15	Fire
Mitchell Bay	Mature	37	25	Fire
Old Franks	Mature	37	61	Fire
Old Franks	Mature	40	30	Fire
Saks Cove	Mature	36	30	Logging
Point Barrie	Mature	38	33	Logging
Point White	Mature	33	30	Logging
South Zarembo Is.	Mature	37	23	Logging
Virgin Bay	Mature	40	122	Logging
West Zarembo Is.	Mature	42	7	Logging
Clark Bay	Old-growth			
	h	35	45	Unknown
Hawk Inlet	Old-growth			
	h	--	Varies	Unknown
Lemon Creek	Old-growth			
	h	--	46	Unknown

¹See Alaback (1982b) for a more complete description of these sites.

²Clearcut = forests less than 40 years old and of logging origin; mature = forests 40-250 years old; old-growth = stands with codominant trees > 250 years old (Alaback 1982a).

³Samples were taken from both control and precommercially thinned sections of the stand.

TABLE 2. Relation of percentage of ground cover to total aboveground biomass of three representative shrub species. Cover estimates are based on averages of 10 to 15 4-m² plots or 30 to 60 1-m² plots. A linear regression model was used.

Shrub Species	B ₀	B ₁	n	r ²	MSE	Range of Cover (%)
4-m ² plots						
<i>Vaccinium alaskaense</i>	2.4659	0.4123	22	0.228	30.563	0-26
<i>Menziesia ferruginea</i>	0.0905	1.5497	22	0.791	2.840	0- 5
<i>Rubus spectabilis</i>	0.5631	0.8025	22	0.555	6.875	0-16
1-m ² plots						
<i>Vaccinium alaskaense</i>	-7.220	17.307	15	0.559	147.33	0-42
<i>Menziesia ferruginea</i>	9.5272	-1.1535	15	0.000	20.865	0- 5
<i>Rubus spectabilis</i>	14.4183	12.5609	15	0.705	50.703	0-66

TABLE 3. Equations for predicting biomass^a of woody shrubs and understory trees, low-growing shrubs, herbaceous vascular plants, ferns, bryophytes, and foliose lichens.

Species	Y_i^b	\hat{B}_0	\hat{B}_1	X_1^c	Units	n	r^2	MSE	Range X
Woody shrubs and understory trees									
<i>Menziesia ferruginea</i>	prod	-3.9782	2.4244	ln dia	mm	24	0.83	0.652	1-24
	wood	-4.1260	3.1899	ln dia	mm	24	0.93	0.472	1-24
	fol	-3.2229	1.9287	ln dia	mm	15	0.79	0.440	1-24
	twig	-7.5778	3.0260	ln dia	mm	10	0.74	1.845	1-24
<i>Oplopanax horridum</i>	wood	-6.7588	3.6530	ln dia	mm	21	0.84	0.710	5-30
	fol	-5.1580	2.8904	ln dia	mm	16	0.89	0.260	5-30
	twig	-4.9413	2.3650	ln dia	mm	18	0.84	0.318	5-30
<i>Ribes laxiflorum</i>	twig	-0.0842	0.0556	dia	mm	6	0.87	0.002	2-7
	wood	-1.8576	3.3567	dia	mm	6	0.80	0.158	2-7
	fol	-3.2735	1.2329	dia	mm	6	0.81	0.158	2-7
<i>Rubus spectabilis</i>	prod	-3.7189	2.8406	ln dia	mm	60	0.72	0.578	1-25
	wood	-2.5536	2.5467	ln dia	mm	35	0.76	0.308	2-25
	fol	-2.0270	1.8840	ln dia	mm	21	0.77	0.382	2-25
	twig	-2.7389	2.0899	ln dia	mm	21	0.86	0.260	2-25
<i>Sambucus canadensis</i>	prod	-4.5228	2.8875	ln dia	mm	18	0.92	0.306	2-29
	wood	-6.0146	3.8064	ln dia	mm	21	0.92	0.570	2-29
	fol	-4.8793	2.9225	ln dia	mm	18	0.92	0.343	2-29
	twig	-6.2614	2.0991	ln dia	mm	20	0.85		
<i>Tsuga heterophylla</i>	biom	-2.3777	2.8080	ln dia	mm	205	0.99	0.123	1-29
	fol	-2.9876	2.2490	ln dia	mm	110	0.97	0.244	1-29
	wood	-3.0539	2.7891	ln dia	mm	110	0.98	0.281	1-29
<i>Vaccinium alaskaense</i> <i>-ovalifolium</i>	prod	-3.3489	1.9657	ln dia	mm	191	0.75	0.673	1-26
	wood	-2.8911	2.7765	ln dia	mm	68	0.92	0.472	1-26
	fol	-2.5927	1.7790	ln dia	mm	16	0.79	0.870	1-26
<i>V. parvifolium</i>	twig	-3.0235	1.5324	ln dia	mm	19	0.74	0.885	1-26
	prod	-3.2121	2.1207	ln dia	mm	27	0.83	0.557	1-21
	wood	-2.5582	3.0842	ln dia	mm	19	0.97	0.334	1-21
	fol	-2.7705	2.0208	ln dia	mm	20	0.75	1.644	1-21
	twig	-3.1062	1.7640	ln dia	mm	14	0.85	0.763	1-21
biom ^d	-0.7809	0.9532	ln cov	%	12	0.82	0.245	1-10	
Low-growing shrubs and herbaceous vascular plants ^e									
<i>Clintonia uniflora</i>	biom	-9.4249	2.4713	ln len	cm	59	0.96	0.042	6-18
<i>Coptis asplenifolia</i>	biom	0.7780	0.3420	cover	%	19	0.87	0.021	2-40
	biom	-1.1096	1.1501	ln cov	%	12	0.71		
						7	0.135	0.135	1-10
<i>Cornus canadensis</i>	biom	-0.6950	0.5360	cover	%	20	0.95	0.032	3-60
	biom	0.2180	0.0440	cover ²	%	12	0.52	0.024	1-10
<i>Lysichiton americanum</i>	biom ^d	-12.40							
		25	3.2564	ln len	cm	38	0.84		
<i>Maianthemum dilatatum</i>						1	0.767	0.767	5-145
	biom	-1.3370	0.4080	cover	%	15	0.93	0.083	1-97
	biom	0.009	0.324	cover	%	9	0.99	0.001	1-15
<i>Moneses uniflora</i>	biom	1.667	0.3950	cover	%	8	0.89	0.150	1-25
<i>Rubus pedatus</i>	biom	2.1030	0.1640	cover	%	19	0.84	0.020	1-60
	biom	1.202	0.0300	cover ²	%	10	0.77	0.007	0-11
<i>Streptopus amplexifolius</i>	biom	-9.6545	2.3971	ln len	cm	26	0.99	0.074	4-91
<i>S. roseus</i> or <i>S. streptopoides</i>	biom	-8.1465	1.9410	ln len	cm	28	0.89	0.000	7-24
	biom	-0.135	0.0950	cover	%	21	0.96	0.191	3-90
	biom	0.021	0.0100	cover ²	%	7	0.70	0.074	3-10
<i>Tiarella trifoliata</i>	biom	-3.0090	0.8030	cover	%	22	0.95	0.145	1-75
	biom	0.7857	0.0379	cover ²	%	13	0.66	0.013	0-10

Table 3 continued

Species	Y_1^b	\hat{B}_0	\hat{B}_1	X_1^c	Units	n	r^2	MSE	Range X
Ferns ^e									
<i>Asplenium viride</i>	biom	-9.3292	2.2520	ln len	cm	30	0.98	0.000	13-42
<i>Athyrium filix-femina</i>	biom	-9.9656	2.3740	ln len	cm	32	0.98	0.000	18-147
<i>Blechnum spicant</i>	biom	-7.4742	1.8480	ln len	cm	78	0.78	0.053	14-56
<i>Dryopteris austriaca</i>	biom	-8.8097	2.2050	ln len	cm	229	0.98	0.000	4-95
<i>Gymnocarpium dryopteris</i>	biom	-9.2541	2.2105	ln len	cm	55	0.97	0.053	5-50
	biom ^d	-3.5235	1.4830	ln cov	%	20	0.97	0.073	5-100
<i>Polystichum munitum</i>	biom	-8.6306	2.2591	ln len	cm	32	0.95	0.090	8-106
<i>Thelypteris phegopteris</i>	biom	-8.9893	2.2815	ln len	cm	13	0.97	0.000	13-27
Bryophytes and foliose lichens									
<i>Stokesiella oregonum</i>	biom	12.8190	1.2330	cover	%	8	0.86	0.028	2-90
<i>Hylocomium splendens</i>	biom	0.4446	1.0968	ln cov	%	30	0.91	0.053	1-90
<i>Jungermannia lanceolata</i>	biom	-6.6614	1.8181	ln cov	%	28	0.89	0.159	1-88
	biom	0.0000	0.7120	cover	%				1-22
<i>Lobaria oregona</i>	biom	-2.7774	1.7255	ln rad	cm	40	0.90	0.207	1-16
<i>Plagiothecium undulatum</i>	biom	-0.6580	0.8800	cover	%	17	0.81	0.950	1-15
<i>Pogonatum macounii</i>	biom	-3.6120	1.7750	cover	%	12	0.94	0.987	1-90
	biom	0.000	0.5710	cover	%				1-3
<i>Rhizomnium glabrescens</i>	biom	7.0710	0.9520	cover	%	13	0.81	1.373	1-80
<i>Rhytidadelphus loreus</i>	biom	0.4195	1.0209	ln cov	%	29	0.87	0.233	1-90

^aBiomass is predicted in grams from least squares estimates of plant biomass from measurements of plant dimensions. Log transformations (natural log) were used when they significantly improved coefficient of determination and decreased mean square error. The model used is indicated in column 5 (X_1). Equations give biomass in grams per shoot or, for regressions based on percentage of ground cover, grams per square meter.

^bProd = annual twigs and foliage, wood = woody biomass (not including annual twigs), twig = annual twigs, fol = leaf blades and petioles, biom = total aboveground biomass.

^cln dia = \log_e of basal shoot diameter, ln cov = \log_e percentage of projected ground cover, ln len = \log_e of shoot or final length, ln rad = \log_e radius of fragment size, cover² = (percent ground cover on 0.1-m² plot)².

^dSource: Ward Brady, Arizona State University, unpublished data.

^eEither herb shoot-length or percentage of ground cover were independent variables, depending on density and vertical dimensionality of the species.

Horizontal shrubs may have a precise cover-biomass relationship. The relationship of *Vaccinium parvifolium* (red huckleberry) growing robustly on an open, sunny site is highly variable, but under a dense overstory canopy, where it is usually decumbent, the relationship is good ($r^2 = 0.82$, Table 3).

Basal shoot diameter was the most precise predictor of biomass for all shrub species, as found in research on shrub biomass in other forest regions (Whittaker and Woodwell 1968),

Stanek and State 1978, Smith and Brand 1983). Shoot height and vigor class, significantly related to biomass when stem diameter was included in the regression equations, were omitted from the final model because of the subjectivity of measuring vigor class and the inefficiency of measuring shoot height in the field.

From 74 to 97 percent of the variation in biomass of the seven woody shrub species sampled was accounted for by basal stem diameter (Table 3). Foliar and annual twig biomass had

the most imprecise relationship and wood biomass the most precise relationship, as twig and foliage biomass often varies with short-term changes in microenvironment and with changes in shrub density.

The proportion of foliage in understory biomass and net annual productivity decreased with increasing stem diameter (Figure 2A). *Oplopanax horridum* (devil's club) and *Sambucus canadensis* (red elderberry) had the highest proportion of foliar biomass, *Vaccinium parvifolium* the lowest. *Oplopanax horridum*, *Sambucus canadensis* and *Rubus spectabilis* (salmonberry) occur in large canopy openings or in clearcuts where they develop large, open canopies. *Vaccinium* species and *Menziesia*, by contrast, tolerate closed canopies as well as clearcut or riparian openings, and they have lower proportions of foliar biomass (Alaback 1982a). *Menziesia ferruginea* and *Vaccinium parvifolium* are apically dominant, often exceeding 3 m and having a large proportion of woody biomass. In contrast, *Ribes laxiflorum* (trailing currant) rarely exceeds 0.5 m in height, creeping across forest openings in a prostrate life-form. The proportion of foliar biomass of these species and the rate of woody biomass accumulation are consistent with differences in life-form and autecology (Figure 2A, B) and with patterns of regression equations reported for shrub biomass in the northeastern United States (Whittaker 1966, Whittaker and Woodwell 1968).

Regression equations for woody biomass varied significantly (Table 5). A *Vaccinium parvifolium* stem 11 mm in diameter had more than 17 times the biomass of an *Oplopanax* stem of the same size (Figure 2B). The three most robust woody species had significantly different regression equations for both y-intercept and slope ($P = 0.95$ and 0.99 , respectively). The most distinct difference between equations occurred in the largest stem size classes. A few species had similar equations, especially for twig and foliage production. *Oplopanax* and *Sambucus* were not significantly different at $P = 0.95$.

Herbaceous species. In contrast to woody shrub species, most herbaceous species showed a consistent relationship between percentage of ground cover and biomass and productivity ($r^2 = 0.84 - 0.95$, $MSE < 0.15$ g; Table 3). Taken as a whole, y-intercepts of herb cover-biomass equations are not significantly different ($P <$

0.95), but slopes are ($P > 0.99$) (Table 5). Several equations have negative intercepts. Separate biomass prediction equations were made from the small range of these species to improve the accuracy of estimates. Plants occupying 0-10 percent ground area were used to achieve adequate sample sizes for some equations, but the equations are most useful in the 0-5 percent range if the coefficient of determination is lower than that with the equation for the full set of data.

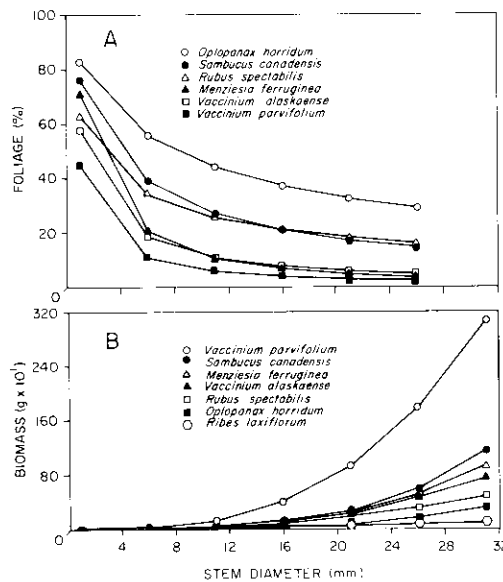


Figure 2. Relation of biomass accumulation to stem size for representative shrub species. (A) Percentage of total shrub biomass contributed by foliage is estimated from regression functions in Table 3. (B) Shrub wood biomass includes bark but not annual twigs.

Slopes of the equations were significantly different ($P = 0.95$) for all species except *Maianthemum dilatatum* (deerberry), *Coptis aspenifolia* (gold thread), and *Moneses uniflora* (single delight), which have a similar slope but different y-intercepts. *Moneses* and *Coptis* are short (< 0.5 dm) evergreen herbs that occur primarily under continuous forest canopies. *Maianthemum* is taller (often > 0.5 dm) and occurs in more open, shoreline forests and in wetland (bog) areas.

Life-form and canopy structure were generally related to biomass. *Tiarella trifoliata* (foam flower) which accumulated the greatest biomass in relation to cover, has a vertical or multilayer (Horn 1971) life-form with short, circular leaves

interspersed along the stem. It occurs primarily in open, wet areas, especially along small streams. *Rubus pedatus*, by contrast, has a low, creeping life-form with intermittent clusters of leaves (monolayer structure) along surficial runners. It occurs in clearcuts and old-growth forests. On the average, 50 percent cover of *Tiarella* had six times the biomass of the same area of *Rubus pedatus* (Figure 3).

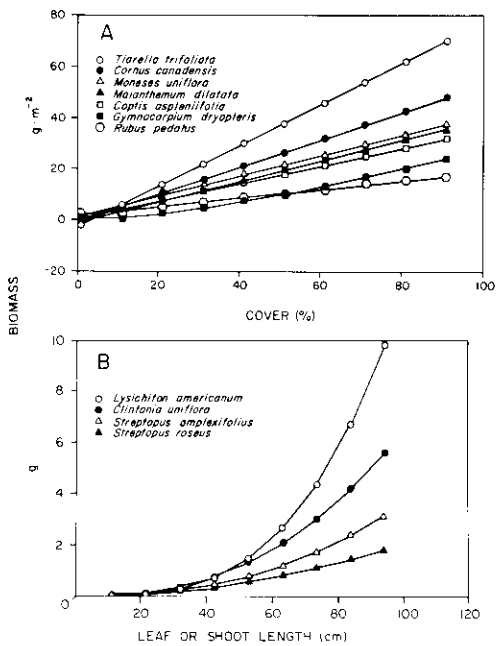


Figure 3. Relation of herb biomass to percentage of ground cover and leaf or shoot length.

Most fern and lily species (*Clintonia*, *Streptopus*, and *Lysichiton*) have a strong vertical component and a highly variable relationship between ground cover and biomass. Shoots of many of these species change orientation with length, from short and almost flat on the ground to large, robust, and nearly vertical. This distribution factor naturally means a less precise relationship of biomass to projected ground cover. For these species, plant shoot height (or frond length) was the best predictor (Figures 3, 4).

Regression equations for several fern and lily species were among the most precise in this study ($r^2 > 0.98$, $MSE < 0.01$ g). As with other herbs, the most significant difference between equations

was not y-intercept, but slope. *Clintonia* and *Lysichiton* have succulent, elongate leaves very different in length (*Clintonia* usually less than 2 dm, *Lysichiton* often more than 10 dm). These species had similar biomass regression equations ($P < 0.95$ for both slope and aspect). The two species of *Streptopus*, owing to their distinct branching patterns, had significantly different slopes and y-intercepts ($P > 0.99$).

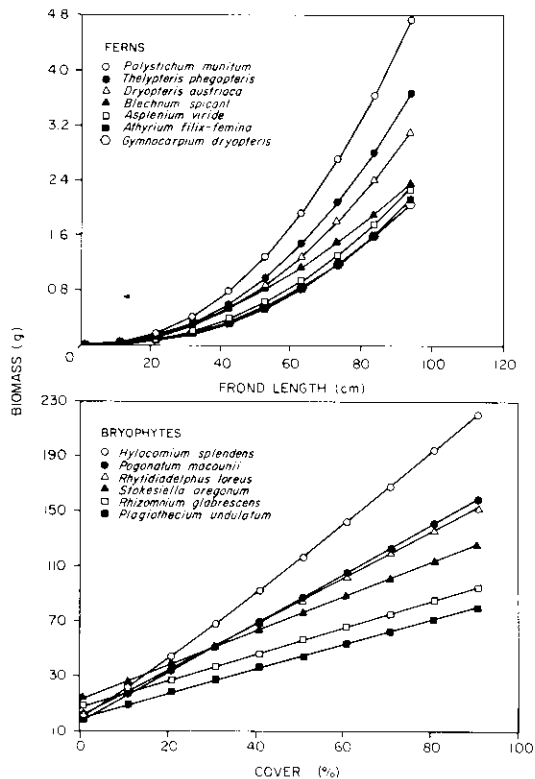


Figure 4. Relation of fern and bryophyte biomass to frond length and percentage of ground cover.

Biomass accumulation of fern species varied widely per unit frond length. *Athyrium* and *Dryopteris*, although similar in leaf morphology, had significantly different biomass equations as an *Athyrium* frond 70 cm long has less than half the biomass of a *Dryopteris* frond of the same length. But *Dryopteris* and *Gymnocarpium*, with distinctly different leaf morphology, had insignificantly different biomass equations. Both species grow under dense *Tsuga heterophylla* canopies where vascular plants are few. All regression equations differed significantly except

those for the three least dense species (*Gymnocarpium dryopteris*, *Athyrium filix-femina*, and *Asplenium viride*).

Bryophytes and lichens. All nine bryophytes and the one foliose lichen sampled showed consistent biomass-cover relationships (Table 3, Figure 4), those for the two feather moss species (*Hylocomium* and *Rhytidiadelphus*) and the liverwort (*Jungermannia*) being curvilinear. Dense carpets of feather mosses are generally older than small patches, a difference in age structure that may account for the nonlinear relationship (higher percentages of cover representing large, older clones), as it does in the small range of the herb-cover equations.

All but one of the groups of regression equations (for *Pogonatum macounii* and *Rhytidiadelphus loreus*) had significantly different y-intercepts ($P < 0.05$). Species that tend to form thick, broad carpets under mature and old-growth forests had the greatest biomass density; shorter, sometimes solitary species (*Rhizomnium glabrescens* and *Plagiothecium undulatum*) that form small, diffuse clumps on specialized substrates like logs and stumps, had the least.

Effects of Phenology and Site

The difference between estimates of percentage of ground cover and biomass made on 29 June, 28 July, and 28 August (86.6, 87.5, and 86.2 kg ha⁻¹) is well within the margin of error of measurement. If the data are typical of the study area, most annual growth of understory vegetation occurs before 1 July. Accordingly, no significant relationship was found between the location or date of sample collection, relative to the beginning or end of the growing season, and the prediction equations (Table 4). A detailed 1-year study of the phenology of biomass and nutrients on a site in the northern end of the study area confirmed that plant ground cover or biomass changed little between 1 July and 1 September (Hanley and McKendrick 1985).

Because site was an insignificant factor in the biomass-dimension regression ($P < 0.05$; Table 4), the equations should provide reasonable estimates of biomass and productivity of plant species in environments similar to those in coastal Alaska. For relationships such as biomass to percentage of cover, additional sampling of specific habitats may yield more precise estimates

(Daubenmire 1968, Payne 1974). Prediction of biomass made from frond length or shoot length of herbs and ferns tended to be the most robust among sites.

TABLE 4. Effects of site, phenology, and year of measurement on biomass regression equations of representative woody shrub, fern, and herb species.

Source of variation	Variation (%)	F Statistic
<i>Vaccinium alaskaense</i>		
Size class (diameter)	69.4	629.0
Sampling site	7.9	9.0
Phenology	0.03	0.3
Year of sampling	0.2	2.0
Residual error	22.4	
<i>Blechnum spicant</i>		
Size class (frond length)	88	387.0
Sampling site	2	3.0
Phenology	1	0.4
Residual error	10	
<i>Cornus canadensis</i>		
Size class (cover)	76	70
Sampling site	2	0.5
Phenology	0	0
Year of sampling	0.3	0.3
Residual error	21	

Sampling Analysis

Vegetation tends to vary most in clearcuts, with patches of vigorously growing and sprouting shrubs occurring beside dense pockets of *Tsuga* or *Picea* regeneration with little understory. Typically, 15 or more 4-m² plots or 60 or more 1-m² plots are needed for a precise estimate of total understory biomass (Figure 5). The same precision in mature forests may require only 10 to 15 4-m² plots or 30 to 40 1-m² plots, yet may yield more accurate estimates because of depauperate vegetation. Most understory species in mature forests are bryophytes and herbs, usually growing at low densities. Only 8 to 10 4-m² plots were needed for precise estimates under old-growth biomass (Figure 5), which had substantially more vegetation than the mature stage and less variation than the clearcut stage.

If we assume that each 1-m² or 4-m² plot represents an independent estimate of understory biomass for a given stand, and that errors in estimates are normally distributed, the number

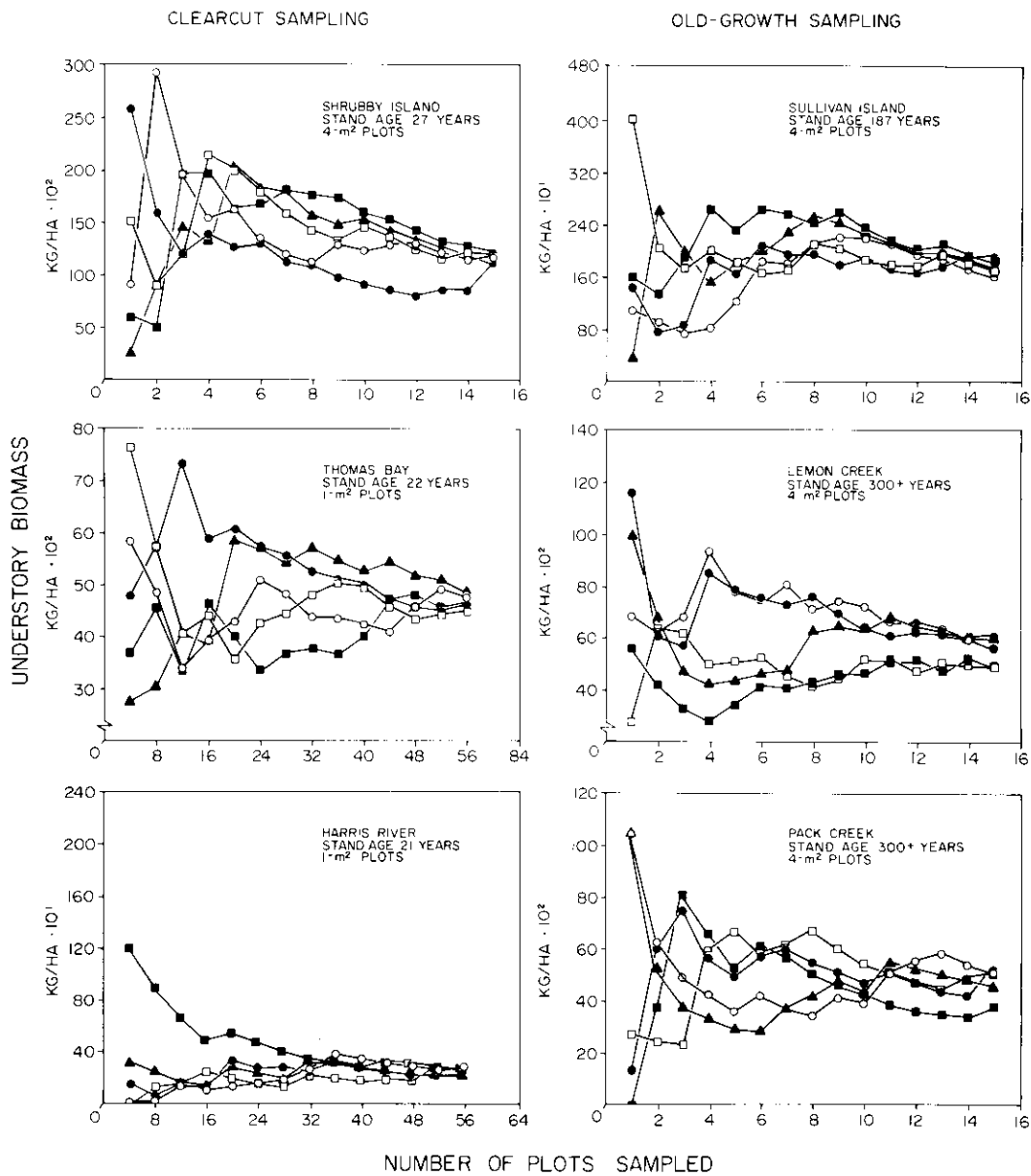


Figure 5. Sampling-area curves for biomass estimation on clearcut and old-growth plots. Five separate runs for each site illustrate the effect on biomass estimates of randomly choosing plots in different sequences.

TABLE 5. Comparison of slopes and intercepts of biomass equations for different species derived from full and reduced regression models.

Biomass component		F	F
Species being compared	df‡	intercepts	slopes
Woody biomass			
<i>Rubus spectabilis</i> , <i>Menziesia ferruginea</i>	4/60	3.47*	0.10
<i>Vaccinium parvifolium</i> , <i>Menziesia ferruginea</i>	4/42	5.13**	11.21**
<i>Vaccinium alaskaense</i> , <i>Ribes laxiflorum</i>	4/71	2.79**	0.70
<i>Vaccinium alaskaense</i> , <i>Rubus spectabilis</i>	4/102	0.03	3.34*
	3/103		
Twig and foliage			
<i>Menziesia ferruginea</i> , <i>Ribes laxiflorum</i> , <i>Rubus spectabilis</i> , <i>Vaccinium alaskaense</i> , <i>V. parvifolium</i>	10/257	0.80	34.73**
<i>Vaccinium parvifolium</i> , <i>Menziesia ferruginea</i>	6/261		
	4/41	2.37	0.88
	3/42		
<i>Menziesia ferruginea</i> , <i>Vaccinium alaskaense</i>	4/181	2.20	0.30
	3/182		
<i>Rubus spectabilis</i> , <i>Ribes laxiflorum</i>	4/55	0.57	8.34**
	3/56		
<i>Rubus spectabilis</i> , <i>Vaccinium alaskaense</i>	4/216	0.57	0.68
	3/217		
Shoot length			
<i>Streptopus roseus</i> , <i>S. amplexifolius</i> , <i>Clintonia</i> <i>uniflora</i> , <i>Lysichiton americanum</i>	8/77	1.13	4.08**
<i>Clintonia uniflora</i> , <i>Lysichiton americanum</i>	5/80		
	4/41	0.32	2.05
	3/42		
<i>Streptopus amplexifolius</i> , <i>S. roseus</i>	4.36	6.46**	6.76**
	3/37		
<i>Clintonia uniflora</i> , <i>Streptopus amplexifolius</i>	4/29	0.06	9.16**
	3/30		
Percentage cover			
<i>Cornus canadensis</i> , <i>Coptis asplenifolia</i> , <i>Tiarella trifoliata</i>	6/60	0.07	6.70**
	4/62		
<i>Cornus canadensis</i> , <i>Tiarella trifoliata</i>	4/43	0.02	6.61**
	3/44		
<i>Coptis asplenifolia</i> , <i>Rubus pedatus</i>	4/37	2.12	28.54**
	3/38		
<i>Rubus pedatus</i> , <i>Tiarella trifoliata</i>	4/40	0.40	32.51**
	3/41		
<i>Cornus canadensis</i> , <i>Maianthemum dilatata</i>	4/36	0.29	5.27**
	3/37		
<i>Maianthemum dilatata</i> , <i>Coptis asplenifolia</i>	4/30	3.82*	0.03
	3/31		
<i>Cornus canadensis</i> , <i>Rubus pedatus</i> , <i>Tiarella trifoliata</i>	6/63	0.39	22.69**
	4/65		

* Significant at P = .095

** Significant at P = 0.99

‡ Degrees of freedom; number of parameters in model/number of observations

of samples for a given level of precision can be estimated from sample variance (Cochran 1963). Estimates are inflated because of the nonrandom distribution of forest vegetation, but still provide a useful index of sampling requirements for various sites.

A strong pattern of change in sampling requirements with stand age is suggested by the variance estimates for 60 stands studied. For the same level of precision, recently logged sites require more plots, by 2 or more orders of magnitude, than mature or old-growth forests. In general, understory biomass varies in proportion to accumulated understory biomass ($r = 0.70$, $P > 0.99$).

Vegetation structure should be considered before assessing how best to estimate biomass by means of regression equations. Forest understory vegetation in coastal Alaska is patchy and nonrandom in distribution, as in other forest regions (Kershaw 1963); therefore, plot size and sampling intensity have important bearing on the adequacy of the sample (Kershaw 1963, 1973; Daubenmire 1968).

The effect of plot size on biomass estimation of coastal Alaskan vegetation has been evaluated on 0.1-m², 1-m², and 4-m² plots. The 0.1-m² plots recommended by Daubenmire (1959) are ideal for herb and moss biomass, quick to measure and reasonably precise for estimates of percentage of ground cover when 30 to 40 are located on a site. Species with coarse-grained spatial patterning, like woody shrubs, have lower variance on 1-m² plots. For herbs, 4-m² plots give less variance than 1-m² plots but require more time for similar precision. The 4-m² plots are most accurate and field efficient for clumps of large woody shrubs such as *Menziesia ferruginea* or *Vaccinium alaskaense*. Overall, 4-m² plots were the most efficient for estimating understory biomass. In recently clearcut sites, 2.6 times more 1-m² than 4-m² plots are needed for measuring biomass to within 10 percent of the mean, yet 30 1-m² plots may take twice as much time to measure as 10 4-m² plots. This ratio is maintained or exceeded with older age classes. If highly precise measurements of large woody shrubs are required, even larger plots may be needed.

Discussion

The tendency for complex, multilayered canopies to accumulate the most biomass and for prostrate monolayer species to have modest accumulation per unit area or stem diameter holds between and within life forms. Tolerance of species to low-level solar radiation is also related to biomass. Herbs growing under dense overstory canopies (i.e. *Moneses uniflora*, *Gymnocarpium dryopteris*) have the least biomass, woody shrubs growing in early seres, as in the riparian zone or in recent clearcuts, have the most biomass (*Rubus spectabilis*, *Sambucus canadensis*).

Even if appropriate equations are selected for a given species, other sources of error may compromise the precision of estimates. In nondestructive sampling, the principal sources are: 1) application of an equation to plants in a different phenological stage than that of the plants used to develop it, 2) differences between microenvironments or the genetics of samples used to develop the equation and of plants to which it is applied, and 3) inadequate or biased sampling design.

The first two sources of error may be easily evaluated for equations developed in this study. Plot data taken in southeast Alaska between 1 July and 1 September at sea level (or equivalent dates at higher elevations) should be within the range of samples used to develop the regression equations. The biomass equations are most likely to apply to data taken within the coastal Alaska *Picea sitchensis*-*Tsuga heterophylla* forest region. Equations for plants invading recently disturbed sites have the greatest potential for error, as clearcuts less than 10 years old and primary successional sites with robust shrub and herb growth were not sampled as thoroughly as other age classes.

Understory species colonize and expand, decay and become extinct over the life of a forest stand (Alaback 1982a, 1982b). When the overstory canopy opens after windthrow, for example, or when it becomes more dense after canopy closure, leaf area and twig production change first. Eventually the distribution and density of shoot size classes within a clone change, through new sprouts or the death of old shoots (Tappeiner 1971, White 1979). Shrub biomass samples for this study were primarily collected from vigorous plants in clearcut or old-growth

areas; therefore, if the equations are used for shrubs dying back under a rapidly closing canopy, overestimates may result. Conversely, foliar biomass and productivity of unusually vigorous shrubs growing in recently disturbed sites may be underestimated.

The advantage in using cover-based biomass equations for shrubs is that many cover estimates can be made in the time required for a few measurements of basal shoot diameter or canopy volume. In recently clearcut vegetation, measurement of shrub shoot diameter commonly took 10- to 15-fold the time required to make estimates of percentage of cover. Separate biomass-cover regression equations are needed for each sere and site if biomass estimates are to be accurate.

The third source of error, the size of nondestructive samples for estimating understory vegetation biomass, has been given little attention despite its importance. Biomass often has an exponential relationship to plant abundance, so that more plots are needed for estimating biomass than are needed for estimating frequency or cover. During the first year of a study of forest succession in southeast Alaska, 40 to 60 1-m² plots were sampled in each stand (Alaback 1982a, 1982b), but 10 to 15 4-m² plots, more field efficient and yielding similar precision, were used in the last 2 years of the study.

In clearcuts or other recently disturbed areas where vegetation tends to be patchy, other sampling schemes may be necessary; 100 or more plots may be needed for achieving the same accuracy that 20 to 30 plots yield in mature or old-growth forests. Double sampling may be more

efficient than single-stage plot sampling on highly variable sites. For example, percentage of ground cover could be measured on a large set of plots, and a subset could be measured for basal diameters of shrubs or trees and shoot lengths of ferns or herbs. A relationship between stem and shoot data and percentage of ground cover could then be developed so that biomass could be estimated for all plots (Cochran 1963, Pieper 1978).

Applicability of the biomass equations in this study to regions outside southeast Alaska is unknown. Many of the species extend into northern California, others (especially bryophytes) into interior Alaska and northern Canada. The relationships may differ in these locations because the continental climates and geochemistry contrast strongly with the cool, wet, maritime climate and the complex geology of southeast Alaska (Andersen 1955). Further research is necessary for assessing the structure and performance of the species along environmental gradients.

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