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Equations for Predicting Above-ground Biomass of Plant Species in Early Successional Forests of the Western Cascade Range, Oregon

Abstract

We present a set of 152 regression equations that predict the above-ground biomass of 38 herb, shrub, and tree species common on early successional (clearcut) sites in the western Cascade Range of Oregon. For many of these species, biomass relationships have not been modeled previously or have not been modeled for early successional sites. Biomass of herbaceous taxa is best predicted by cover, while biomass of woody species is best predicted by stem diameter and/or length. We discuss how relationships between biomass and plant size vary with site age among species of diverse growth form and life history. We supplement best-fit models with alternative equations that are easier to implement in the field or that are less sensitive to sources of variation associated with time since disturbance. To minimize the misapplication of equations, we report the dimensional ranges of all plant variables measured, whether or not they are explicitly modeled.

Introduction

There are many ways to sample or compare the relative abundance of plant species. Frequency, canopy cover, stem density, and basal area are commonly used because they are simple to measure or estimate in the field. Where taxa are of similar growth-form (e.g., trees in a forest, graminoids in a meadow), simple measures of abundance may effectively depict the relative importance of species. Where plants are of markedly differing stature, however, simple measures of abundance may provide a poor basis for comparison among species or for describing community-level attributes such as species diversity (Magurran 1988). For example, co-occurring forest herb, shrub, and tree species, each with the same canopy cover, are likely to differ in how they utilize soil water, cycle nutrients, contribute to community structure, or provide resources (food and habitat) for wildlife. Above-ground biomass may, for many purposes, more effectively indicate the relative importance of taxa in such physiognomically diverse communities.

Directly determining plant biomass is labor-intensive, time-consuming, and destructive, requiring harvesting, sorting, drying, and weighing of samples. Such destructive techniques are unacceptable in experimental or long-term studies where plants cannot be removed from sample plots. As an alternative, an indirect, regression

approach—allometric or dimensional analysis—is commonly used to predict biomass from attributes that can be measured easily. Dimensional analysis has been applied widely in silviculture and mensuration to estimate tree growth and volume (e.g., Spurr 1952, Walters et al. 1985, Smith 1986, Hann et al. 1987, Husch et al. 1993), and in ecological studies of community structure and function (e.g., Whittaker and Woodwell 1968, Whittaker et al. 1974, Whittaker and Marks 1975, Grier and Logan 1977).

Although it is rarely applied in such situations, the use of dimensional analysis has particular value for predicting plant biomass in permanent plot studies of succession where destructive sampling is not possible, but biomass is an appropriate indicator of dominance. In this paper, we present a set of regression equations for estimating above-ground biomass of plant species common on recent, post-harvest sites in the western Cascade Range of Oregon. The equations were developed for long-term field experiments on species' interactions during succession in *Pseudotsuga menziesii* (Douglas-fir) forests (Halpern et al. 1992, Halpern et al. *in press*). Although early successional change has been well-documented in these forests (Dyrness 1973, Halpern 1988, 1989, Schoonmaker and McKee 1988, Halpern and Franklin 1990, Halpern and Spies 1995), plant biomass has rarely been used to describe the chang-

ing abundances of species (but see Gholz et al. 1985). This may reflect the paucity of equations available to predict biomass of many plant species (Gholz et al. 1979, Alaback 1986, 1987, Means et al. 1994) and the inherent limitations of these equations.

A problem common to all dimensional analysis is that regression models developed for a particular study may be applicable only to a narrow range of environments, stand ages, plant sizes, or phenological states (Alaback 1986, 1987, Means et al. 1994). Although we do not examine all plant species common to post-harvest sites in the Pacific Northwest, many in our list are widely distributed in western Oregon and Washington. Nonetheless, our equations are most appropriate for low elevation, early successional (1- to 3-yr-old) sites of the central, western Cascade Range of Oregon. Because local environments and plant form change rapidly after forest harvest, for many species we provide separate equations for each successional year.

A second, pervasive problem exists in the literature on dimensional analysis. Authors commonly report the dimensional ranges of the independent variables used in regression equations for the plants destructively sampled, but neglect to document the dimensional ranges of other potentially important variables. For example, the diameter range of the plants used in constructing a diameter-based equation is reported, but the range of stem heights is often omitted. This creates two problems. First, although height may have varied minimally within the harvested population, it may vary in other populations. Second, without knowledge of the full range of plant dimensions for variables other than those utilized in models, it is easy to inappropriately apply equations to other populations. To minimize the potential for misapplication of our equations, we report the dimensional ranges of all variables measured, whether or not they are explicitly used.

Our primary goal is to provide researchers with a set of biomass equations for species that are common after harvest of *Pseudotsuga* forests in the western Cascade Range of Oregon. Biomass relationships for many of these species either have not been modeled previously or have not been modeled for early successional sites. We also illustrate how relationships between biomass and other plant attributes can vary with time among

species of diverse growth form and life history. To meet the diverse needs of potential users, we have taken two approaches. First, we identify the independent variable or variables that best predict above-ground biomass for each species. Second, we develop alternative equations for most species that, although less precise, are based on variables that are more easily or quickly measured in the field (e.g., plot-level cover rather than individual stem diameters). Under conditions where precise estimates of biomass are not critical or the best predictors have not been measured, these latter equations can be used with known explanatory power.

Methods

Study Site

Destructive sampling was conducted over a 3-yr period on a clearcut and burned site in which we are studying plant species' interactions during early succession (Halpern et al. 1992, Halpern et al. *in press*). The 4 ha study site lies on a gentle, east-facing slope at 730 m elevation in the Blue River Ranger District of the Willamette National Forest, Oregon, ca. 25 km south of the H. J. Andrews Experimental Forest. Prior to harvest in 1991, the site supported a mature to old-growth forest dominated by *Pseudotsuga menziesii* in the upper canopy and *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western red cedar) in the lower and sub-canopies. Understories were dominated by *Rhododendron macrophyllum* (Pacific rhododendron), *Gaultheria shallon* (salal), and *Berberis nervosa* (Oregon grape). The forest was clearcut logged in late May and early June 1991 and broadcast burned on 11 September 1991. In Table 1 we present frequency and cover data for species most common in the original forest and for the 3 yr during which we destructively sampled after harvest. Nomenclature follows Hitchcock and Cronquist (1973).

The climate is maritime with mild, wet winters and warm, dry summers. Annual precipitation on the nearby H. J. Andrews Experimental Forest averages 2302 mm, but only 6% falls between June and August (Bierlmaier and McKee 1989). Average minimum temperatures range from -5.5°C in January to 11.9°C in August; average maxima range from 5.5°C in January to 23.3°C in July. The growing season (frost-free period) av-

TABLE 1. Frequency and mean cover of principal plant species on the study site prior to (1990) and for three growing seasons after harvest. Only species with frequencies > 25% for at least one sampling date are listed.

Species	1990		1992 (year 1)		1993 (year 2)		1994 (year 3)	
	Freq ^a (%)	Cover (SE) ^b (%)	Freq (%)	Cover (SE) (%)	Freq (%)	Cover (SE) (%)	Freq (%)	Cover (SE) (%)
Colonizing Annual and Biennial Herbs								
<i>Cirsium vulgare</i>	0	0.0(0.0)	4	0.2(0.2)	4	t	76	0.5(0.1)
<i>Collomia heterophylla</i>	0	0.0(0.0)	0	0.0(0.0)	16	0.3(0.2)	36	2.1(0.9)
<i>Conyza canadensis</i>	0	0.0(0.0)	0	0.0(0.0)	76	1.5(1.0)	92	4.4(2.2)
<i>Crepis capillaris</i>	0	0.0(0.0)	0	0.0(0.0)	4	t	60	1.4(0.4)
<i>Epilobium paniculatum</i>	0	0.0(0.0)	40	0.6(0.2)	100	26.9(2.3)	100	20.3(4.9)
<i>Lactuca serriola</i>	0	0.0(0.0)	0	0.0(0.0)	36	0.2(0.1)	48	0.9(0.5)
<i>Madia gracilis</i>	0	0.0(0.0)	0	0.0(0.0)	4	t	28	0.3(0.1)
<i>Senecio sylvaticus</i>	0	0.0(0.0)	4	t	100	11.6(1.3)	60	0.3(0.2)
Colonizing Perennial Herbs								
<i>Anaphalis margaritacea</i>	4	t	0	0.0(0.0)	12	t	32	0.3(0.1)
<i>Epilobium angustifolium</i>	4	0.1(0.1)	52	1.0(0.3)	100	6.0(2.3)	96	5.9(2.7)
<i>Epilobium watsonii</i>	0	0.0(0.0)	0	0.0(0.0)	84	0.5(0.2)	80	0.9(0.2)
<i>Gnaphalium microcephalum</i>	0	0.0(0.0)	0	0.0(0.0)	68	0.8(0.5)	100	4.2(1.8)
<i>Lupinus latifolius</i>	4	t	20	0.2(0.1)	40	2.1(1.1)	36	0.8(0.5)
Forest Herbs								
<i>Goodyera oblongifolia</i>	28	0.1(0.1)	0	0.0(0.0)	0	0.0(0.0)	0	0.0(0.0)
<i>Hieracium albiflorum</i>	12	0.1(0.1)	0	0.0(0.0)	12	0.1(0.0)	60	0.4(0.1)
<i>Frientalis latifolia</i>	32	0.3(0.2)	68	0.2(0.1)	72	0.6(0.2)	72	2.0(0.6)
<i>Viola sempervirens</i>	72	3.2(0.8)	48	0.2(0.1)	48	0.9(0.3)	68	0.8(0.3)
Forest Shrubs and Understory Trees (< 1.4 m tall)								
<i>Berberis nervosa</i>	84	26.9(4.4)	64	0.8(0.3)	80	4.7(1.0)	80	7.7(1.9)
<i>Gaultheria shallon</i>	88	39.4(6.2)	24	0.2(0.2)	64	0.6(0.3)	76	1.6(0.4)
<i>Linnaea borealis</i>	72	4.7(1.1)	0	0.0(0.0)	0	0.0(0.0)	4	t
<i>Pseudotsuga menziesii</i>	24	t	0	0.0(0.0)	0	0.0(0.0)	72	0.1(0.0)
<i>Rhododendron macrophyllum</i>	60	40.0(8.5)	16	0.2(0.1)	24	1.8(0.8)	24	2.6(1.3)
<i>Rubus ursinus</i>	36	2.1(0.8)	32	0.7(0.5)	52	4.8(2.0)	60	5.9(2.1)
<i>Tsuga heterophylla</i>	52	4.7(3.1)	0	0.0(0.0)	0	0.0(0.0)	36	t

^a Frequency of occurrence among sample plots. Pre-harvest (1990) values are based on 225 permanent, 1 m² sample plots; post-harvest (1992-1994) values are based on 25 randomly chosen, unmanipulated (control) plots.

^b Mean canopy cover (with standard error of the mean); t = trace cover (<0.1%).

erages 134 days, but is extremely variable (Bierlmaier and McKee 1989).

Field and Laboratory Methods

We sampled during each of the first three growing seasons (1992-1994) after logging. Plants were harvested on the following dates: 26-30 July and 4-6 August 1992; 23-24 July and 11, 18 and 22 August 1993; and 8-10 August 1994. Two types of plant measurements were taken: (1) measurements of single, above-ground stems to develop individual, stem-based equations, and (2) integrative measurements of species from within 1 x 1 m sample plots to develop plot-based equations.

In many instances, plants used to develop stem-based equations were obtained from the same plots used to generate plot-based equations. Minimum sample sizes for most equations were 10 per species; more commonly, 20 or more samples per species were obtained.

We chose independent variables that we anticipated would be good predictors of above-ground biomass and that were fairly easy to estimate or measure in the field. For individual stems, these variables included visual estimates of canopy cover, stem basal diameter measured with a caliper (primarily woody plants), stem length (base to tip), and number of primary shoots (main branches)

per above-ground stem. For plot-level measures, variables included canopy cover, stem density, mean basal diameter of stems (an average of the individual stems measured), and modal stem length (a visual estimate). Because the presence of flowers or fruits influences the relationship between plant size and biomass, we noted the phenological state of all plants; plants were classified as all vegetative, some in flower and/or fruit, and all in flower and/or fruit. Herbivory can also influence plant architecture and the allocation of biomass to foliage, branches and stems. For most species, we observed little direct evidence of herbivore damage, however plants that were obviously browsed were not sampled. Thus, our equations may not be appropriate for sites where herbivory is common.

After plants were measured they were clipped at the ground surface, placed in paper bags, and transported to drying ovens. Samples were dried at ca. 55-60°C for 5-9 days. During this time a subset of the heaviest bags were weighed periodically to insure that stable dry weights were obtained. To minimize absorption of moisture during cooling, paper bags and plants were placed in large plastic bags before they were weighed. All samples were weighed to the nearest 0.01 g.

Analytical Methods

Regression equations were developed using the linear and multiple linear regression procedures of MGLH (Multivariate General Linear Hypothesis) of SYSTAT 5.03 (Wilkinson 1990). We had two primary objectives in our modeling approach: (1) to identify the independent variable(s) that best predicted species' above-ground biomass, and (2) to develop additional equations using variables that are more easily or quickly measured in the field (e.g., plot-level cover rather than stem heights and diameters).

For each species, raw data were graphed to visually assess the relationships between biomass and the independent variables. Using both raw and transformed data, biomass was first modeled as a linear function of each independent variable, followed by stepwise addition of one or more variables if they were shown to be significant (by a t-statistic, $p < 0.05$; Wilkinson 1990). At each step, we examined normal probability plots of residuals, and plots of studentized residuals vs. predicted values to test compliance of the mod-

els with the basic assumptions of least-squares regression: that values of the dependent variable are normally distributed about corresponding values of the independent variable, and that the variance of the dependent variable is homogeneous for values of the independent variable (Sokal and Rohlf 1981). Transformations of independent and dependent variables were chosen subjectively using the criteria of Sabin and Stafford (1990). Except for rare cases, logarithmic and square root transformations produced the best models (Appendix 1). Corrections for logarithmic bias were made for log-log equations (Baskerville 1972, Sprugel 1983).

Results and Discussion

A total of 152 regression equations were developed for 38 taxa that are common on early successional, post-harvest sites in the western Cascade Range of Oregon (Appendix 1). The species represent seven broad groups of plants that vary in growth form and successional origin: (1) colonizing annual and biennial herbs, (2) colonizing perennial herbs, (3) colonizing tall shrubs, (4) forest herbs, (5) forest low shrubs and sub-shrubs, (6) forest tall shrubs and understory hardwood trees, and (7) coniferous tree seedlings. For the full set of 152 equations, the median coefficient of determination (R^2) was 0.933 and the range was 0.462-0.997 (Appendix 1). For the 70 primary equations representing the best predictors for each combination of species-by-site age-by-equation type (those with asterisks in Appendix 1), the median R^2 was 0.951 and the range was 0.556-0.997. For each plant group we briefly describe the relationships between plant biomass and form, and how these relationships vary among species and as a function of site age.

The colonizing annual and biennial herbs include winter-annuals that germinate in fall, overwinter as rosettes, and bolt in spring (e.g., *Epilobium paniculatum* and *Senecio sylvaticus*); spring-germinating annuals (e.g., *Conyza canadensis*); and facultative biennials that flower their first year or remain as basal rosettes and flower the second year (e.g., *Cirsium vulgare* and *Lactuca serriola*). Biomass equations were not previously available for a number of these species: *Agoseris grandiflora*, *Conyza canadensis*, *Crepis capillaris*, *Lactuca serriola*, and *Madia gracilis*.

For many taxa in this group, above-ground biomass per stem is predicted well by canopy cover (range of R^2 of 0.671-0.986, Appendix 1), although addition of basal diameter or stem length often improves the relationship (range of R^2 of 0.886-0.986, Appendix 1). However, for some species (*Senecio* and *Conyza* in particular), plant allometry changes with successional time producing different relationships between biomass and cover. For example, stem diameter and height of *Senecio* and *Conyza* decrease with site age (C. B. Halpern, unpublished data) resulting in decreasing plant biomass for a given canopy cover (Figure 1). Consequently, for these species we recommend the use of cover-based equations only on sites with ages similar to those for which equations were developed. Equations that model plant biomass as a function of length and diameter are less responsive to site age (Figure 2) and have R^2 values comparable to cover-based equations (range of 0.814-0.978, Appendix 1). Thus, they have broader applicability. Our results suggest that for most annual and biennial colonists, equations based solely on stem length or basal diameter are poorer than those based on cover. However, for species with greater variation in height than in cover (e.g., *Lactuca serriola*), length is a better predictor of biomass (Appendix 1). The two most common annuals in these early successional communities, *Epilobium paniculatum* and *Senecio sylvaticus*, have been modeled previously (Gholz et al. 1979, Means et al. 1994). Comparability with our equations varies by species, parameter modeled, and site age. For example, our first-year, cover-based equation for *Epilobium* predicts four times the biomass predicted by an equation for an older site (Means et al. 1994). As for *Senecio* and *Conyza*, plants on younger sites (*i.e.* years 1 and 2) have thicker and taller stems than do plants on older sites, resulting in higher plant biomass for a given canopy cover. Predictions of our length-based equations are more comparable with those of Gholz et al. (1979) because length better captures this change in plant allometry with site age.

The group of colonizing perennial herbs includes relatively short-lived species (e.g., *Gnaphalium microcephalum*) and longer-lived taxa that resprout from roots or rhizomes for many years after harvest (e.g., *Epilobium angustifolium*, *Lotus crassifolius*, *Lupinus latifolius*, and *Pteridium aquilinum*) (Halpern 1988, 1989). Biomass equations were not previously available for many of

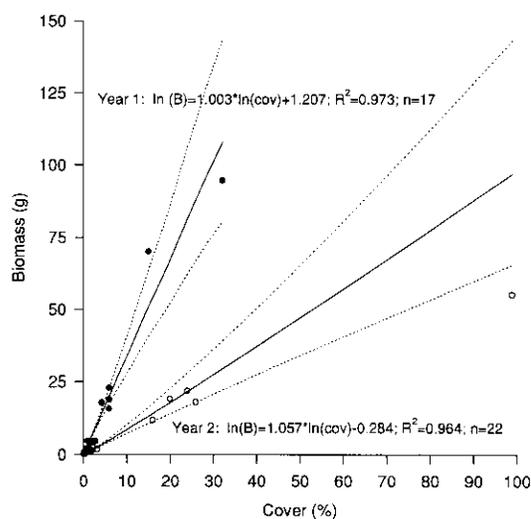


Figure 1. Predicted above-ground biomass (B , in grams) of *Senecio sylvaticus* as a function of plant canopy cover (cov, percentage of a 1 m^2 plot), 1 yr (solid circles) and 2 yr (open circles) after logging and burning. Biomass is plotted only for the range of covers sampled. Dotted lines delimit the 95% confidence intervals. See Appendix 1 for summary statistics and ranges of plant dimensions.

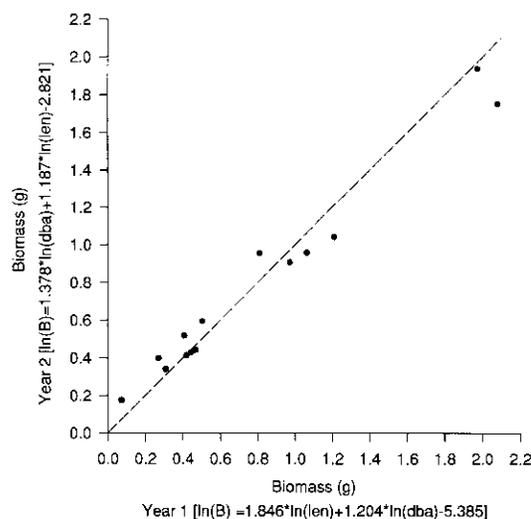


Figure 2. The relationship between the above-ground biomass of *Senecio sylvaticus* predicted for first (X axis) and second (Y axis) year plants. The dashed line is an isoline of equal biomass: that points deviate minimally from this line suggests that biomass predicted by diameter and height varies little between years. The diameters and lengths used to generate the predicted values are from plants measured 3 yr after harvest. See Appendix 1 for summary statistics and ranges of plant dimensions.

these taxa: *Agrostis* spp., *Campanula scouleri*, *Equisetum telmateia*, *Gnaphalium microcephalum*, and *Lotus crassifolius*.

As with the annuals and biennials, variation in the above-ground biomass of colonizing perennials is largely explained by canopy cover (range of R^2 of 0.837-0.991, Appendix 1). The addition of stem length consistently improves the model (range of R^2 of 0.875-0.994, Appendix 1). However, for some species (e.g., the fern *Pteridium aquilinum*; Figure 3), biomass is predicted equally well or better by length than by cover (Appendix 1). Alaback (1987) observed a similar pattern for ferns in southeastern Alaska and attributed the greater explanatory power of length to changes in frond orientation with plant size (i.e. fronds orient more vertically as they elongate).

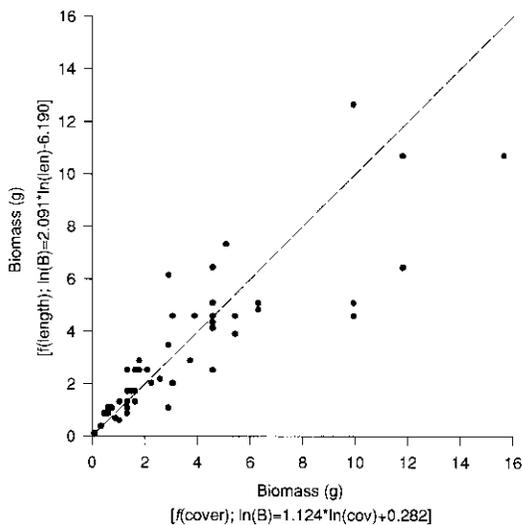


Figure 3. The relationship between the above-ground biomass of *Pteridium aquilinum* predicted by canopy cover (X axis) and total frond length (Y axis). The dashed line is an isoline of equal biomass as a function of cover and length. The values of cover and length used to generate the predictions are those of the 58 individual stems used to develop the models. See Appendix 1 for summary statistics and ranges of plant dimensions.

Several of the perennial herbs in this group (*Epilobium angustifolium* in particular) are extremely plastic in growth form, displaying large variation in height and branching pattern (see ranges for numbers of shoots/plant, Appendix 1). Equations based on cover capture the variation

associated with lateral branching, but not the variation associated with changes in allocation to stems and branches or to changes in plant height. Thus, these equations should be applied with caution. For example, it is unclear what accounts for the greater biomass predicted by our equations developed from shorter (1-77 cm tall), first- and second-year plants (Appendix 1) compared with an equation developed for taller plants (14-178 cm) on an older clearcut site (S. Acker and M. Easter, unpublished data).

The group of colonizing tall shrubs are primarily seed bank species that are stimulated to germinate by removal of the tree canopy, physical soil disturbance, or fire. *Arctostaphylos columbiana*, *Ceanothus sanguineus*, *C. velutinus*, *Ribes lobbii*, *Rubus leucodermis*, and *Rubus parviflorus* all belong to genera in which buried seeds lie dormant for periods ranging from decades to centuries (Quick 1956, Gratkowski 1962). Most of the first-year plants sampled were seedlings, although some stems of *Rubus parviflorus* originated from sprouting rhizomes present in locally disturbed sites of the former forest. Biomass regression equations had not been developed previously for *Arctostaphylos columbiana*, *Ribes lobbii*, *Rubus leucodermis*, and *Sambucus cerulea*. For the remaining species, the few existing equations (e.g., Gholz et al. 1979, Means et al. 1994) are inappropriate for small-statured or young plants. Thus, our diameter-based equation for 1- and 2-yr-old *Ceanothus sanguineus* predict half the biomass of that predicted by an equation developed on a site with older, taller stems (Means et al. 1994).

Typically, above-ground biomass of tall shrubs in these forests is best predicted by stem basal diameter (e.g., Gholz et al. 1979, Alaback 1986, Means et al. 1994). With one exception (*Ceanothus velutinus*), the best equations for predicting biomass of colonizing shrubs in our study were based on diameter and/or height (range of R^2 of 0.945-0.997, Appendix 1). Simple cover-based equations are also sufficient for many species in years 1 and 2 (range of R^2 of 0.625-0.990, Appendix 1) reflecting the large proportion of biomass in foliage relative to stem for very young plants. However, cover-based equations should not be applied to plants older than 2 yr.

The group of common forest herbs contains four species that typically occur with high

frequency, but low cover (Table 1). Following harvest they resprout from deep root systems (*Viola sempervirens* and *Hieracium albiflorum*) or tubers (*Trientalis latifolia*), or survive locally in protected microsites (*Galium triflorum*) (McLean 1968, Halpern 1989, J. A. Antos, unpublished data). Existing equations for these species are not specific to early successional sites; rather, they encompass a range of seral stages (Means et al. 1994, S. Acker and M. Easter, unpublished data). Three of the four species show little variation in height, thus, biomass is best predicted by canopy cover (range of R^2 of 0.905-0.985, Appendix 1). For *Hieracium*, which produces a tall flowering stalk from a basal rosette of leaves, cover plus length are the best predictors of biomass.

The group of low-growing forest shrubs includes two typically dominant species, *Berberis nervosa* and *Gaultheria shallon*, and two subordinate sub-shrubs that are often released by removal of the tree canopy, *Rubus ursinus* and *Whipplea modesta* (Halpern 1989). Equations exist for each species (Means et al. 1994), but these represent older clearcut sites or mature forest.

Berberis nervosa and *Gaultheria shallon* show little within-population variation in height during the first, post-harvest growing season, and biomass is adequately predicted by cover (R^2 of 0.980 and 0.956, respectively, Appendix 1). In subsequent years, however, variation in plant height increases. Thus, the addition of modal height improves the model (Appendix 1). Because these sclerophyllous, evergreen shrubs allocate resources to leaves and stems differently under open and closed canopies (e.g., Gholz et al. 1985, Alaback 1986), application of these equations should be limited to clearcut or burned sites of similar age, or to plants of similar stature growing in full-sun conditions. Cover-based equations developed in older clearcuts (Gholz et al. 1979) or mature/old-growth forest (Means et al. 1994, S. Acker, unpublished data) where plants are typically taller, predict significantly higher plant biomass than do our equations.

Rubus ursinus and *Whipplea modesta* are prostrate, stoloniferous taxa that typically show little variation in height; biomass is well predicted by cover (range of R^2 of 0.905-0.985, Appendix 1). For both species, greater predicted biomass with site age (1 vs. 3 yr; Figure 4) suggests that on young, open sites biomass accumulates in woody

stems with time. That equations developed for significantly older clearcuts (17-30 yr) or mature forest (145 yr) (Means et al. 1994, S. Acker and M. Easter, unpublished data) predict lower biomass than do our equations suggests that factors other than site age—for example, light availability—affect the accumulation and distribution of above-ground biomass.

The two most common tall shrub and hardwood tree species on our site, *Rhododendron macrophyllum* and *Castanopsis chrysophylla*, are disturbance-tolerant taxa that resprout from adventitious buds at the bases of stems, producing dense, multi-stemmed individuals after logging and burning (Gholz et al. 1985, Halpern 1989). Naturally regenerating *Pseudotsuga menziesii* seedlings were also common. For all three woody species, basal diameter or stem length individually explain most of the variation in stem biomass (range of R^2 of 0.845-0.971, Appendix 1); inclusion of both parameters improves predictions (range of R^2 of 0.895-0.986, Appendix 1). Although biomass predicted by diameter and length are correlated in these species, the strength of this relationship tends to decline with time (e.g., *Rhododendron*, Figure 5) as the allocation of resources to diameter and height growth increasingly vary with time since disturbance. Comparisons with other equations indicate that for stems of equal diameter, predicted biomass increases with site age (cf. equations in Appendix 1, Gholz et al. 1979, Means et al. 1994).

Conclusions

Simple measures of plant abundance (canopy cover) or size (stem diameter or length) can be used to accurately predict the above-ground biomass of herb, shrub, and tree species common on early successional sites following harvest of *Pseudotsuga* forests. Biomass of herbaceous taxa is effectively predicted by cover, and biomass of woody species by stem diameter and/or length. Plant form changes rapidly during early succession, thus for many species, equations may differ from year to year. Alternative sets of variables (e.g., diameter plus length rather than cover), or the addition of one or more variables to simpler models, produce equations that are less sensitive to the sources of variation associated with site age or plant form. These results support Alaback's (1987) contention that some of the difficulties in

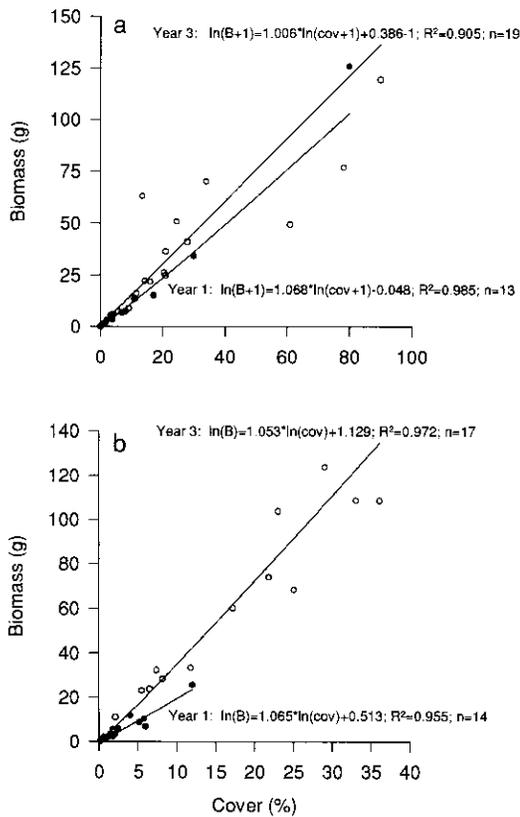


Figure 4. The relationship between total above-ground biomass (B, in grams) and plot-level cover (cov, percentage of a 1 m² plot), 1 yr (solid circles) and 3 yr (open circles) after harvest for (a) *Rubus ursinus* and (b) *Whipplea modesta*. See Appendix 1 for summary statistics and ranges of plant dimensions.

using site- or area-specific regression equations can be overcome by predicting biomass with multiple variables. Additional research is needed to understand how allocation of biomass to foliage, height, and diameter growth vary in response to the rapid changes in physical and biotic environment that characterize early successional sites.

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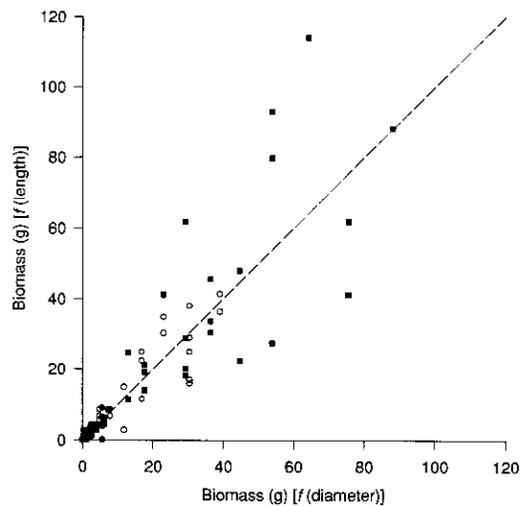


Figure 5. The relationship between the above-ground biomass of *Rhododendron macrophyllum* predicted by stem basal diameter (X axis) and stem length (Y axis), for stems sampled 1 (solid circles), 2 (open circles), and 3 yr (solid squares) after harvest. The dashed line is an isoline of equal biomass predicted by cover and length. The values of diameter and length used to generate the predictions are from the individual stems destructively sampled to develop each model. See Appendix 1 for model form, coefficients, summary statistics, and ranges of plant parameters.

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APPENDIX 1. Equations (with statistics and data ranges) that predict total above-ground biomass of 38 post-harvest plant species. Blanks in data range columns indicate that measurements were not appropriate for the species of interest. Dashes (—) indicate parameter was not measured. Asterisks (*) adjacent to site age denote the primary equations for each species-by-site age-by-equation type (I, P, B) combination—that with the highest coefficient of determination (R^2) (but see footnote j for *Agoseris grandiflora*).

Site age ^a	Type ^b	Equation ^c	R^2	n	MSE	Data range					
						Cover (%) ^d	Basal diameter (cm) ^e	Length (cm) ^f	No. shoots/plant ^g	Stem density (no./m ²) ^h	P ⁱ
Colonizing Annual and Biennial Herbs											
<i>Agoseris grandiflora</i> (large-flowered agoseris)											
3	I	$\ln(B)=1.223*\ln(\text{cov})+0.363$	0.873	15	0.236	0.1-1.5		10-30 ^e			V
3	I	$\text{sqr}(B)=2.314\text{sqr}(\text{cov})-0.513$	0.671	20	0.287	0.1-2.1		25-79			VF
3	I	$\ln(B)=2.826*\ln(\text{len})-9.647$	0.462	20	0.739	0.1-2.1		25-79			VF
<i>Cirsium vulgare</i> (common thistle)											
1	I	$\ln(B)=1.478\ln(\text{cov})+0.053$	0.952	11	0.157	0.8-27		2.0-120	1-3		VF
1	I	$\ln(B)=0.960*\ln(\text{len})+0.151$	0.857	11	0.465	0.8-27		2.0-120	1-3		VF
<i>Collomia heterophylla</i> (varied-leaf collomia)											
1	P	$\ln(B+1)=0.820\ln(\text{cov})+0.717$	0.923	18	0.055	0.6-15		—	—		F
<i>Conyza canadensis</i> (horseweed)											
1	I	$\ln(B)=0.888*\ln(\text{cov})+1.266$	0.670	27	0.601	0.2-16	0.1-1.1	35-165	1-10		VF
1	I	$\ln(B)=0.618\ln(\text{cov})+1.783*\ln(\text{len})-6.381$	0.886	27	0.217	0.2-16	0.1-1.1	35-165	1-10		VF
1	I	$\ln(B+1)=4.280*\ln(\text{dba}+1)$	0.684	26	0.308	0.2-16	0.1-1.1	35-165	1-10		VF
1	I	$\ln(B)=2.693*\ln(\text{len})-9.679$	0.634	27	0.667	0.2-16	0.1-1.1	35-165	1-10		VF
1	I	$\ln(B)=1.298*\ln(\text{dba})+1.326*\ln(\text{len})-3.177$	0.814	26	0.357	0.2-16	0.1-1.1	35-165	1-10		VF
2	I	$\ln(B+1)=2.988*\ln(\text{cov}+1)+0.237$	0.918	17	0.059	0.1-1.4	0.1-0.8	9-140			VF
2	I	$\ln(B)=0.507\ln(\text{cov})+1.582*\ln(\text{len})-5.516$	0.977	17	0.055	0.1-1.4	0.1-0.8	9-140	—		VF
2	I	$\ln(B)=2.748*\ln(\text{dba})+3.222$	0.945	25	0.218	0.1-1.4	0.1-0.8	9-140	—		VF
2	I	$\ln(B)=2.087*\ln(\text{len})-8.193$	0.963	25	0.148	0.1-1.4	0.1-0.8	9-140	—		VF
2	I	$\ln(B)=1.145*\ln(\text{dba})+1.266*\ln(\text{len})-3.668$	0.978	25	0.092	0.1-1.4	0.1-0.8	9-140	—		VF
1	P	$\ln(B)=0.919\ln(\text{cov})+1.132$	0.737	24	0.559	0.2-16	0.1-1.1	35-165	1-10	1	VF
<i>Crepis capillaris</i> (smooth hawkbeard)											
1	I	$\ln(B)=1.182\ln(\text{cov})+0.086$	0.814	12	0.147	0.3-3.0		3.0-57			VF
3	I	$\ln(B)=0.674\ln(\text{len})-1.923$	0.556	27	0.640	—		1.0-80			VF
<i>Epilobium paniculatum</i> (autumn willow-herb)											
1	I	$\ln(B)=1.118*\ln(\text{cov})+0.351$	0.872	24	0.366	0.2-22	0.1-1.0	15-95			VF
1	I	$\ln(B)=1.154\ln(\text{cov}+1)+0.978*\ln(\text{dba})+0.451$	0.948	23	0.161	0.2-22	0.1-1.0	15-95			VF
1	I	$\ln(B)=1.815*\ln(\text{dba})+1.244*\ln(\text{len})-1.678$	0.899	23	0.312	0.2-22	0.1-1.0	15-95			VF
3	I	$\text{sqr}(B)=3.597*\text{sqr}(\text{dba})-0.821$	0.846	29	0.066	—	0.1-0.6	4.0-80			VF
3	I	$\ln(B)=2.335*\ln(\text{len})-8.922$	0.930	29	0.307	—	0.1-0.6	4.0-80			VF
3	I	$\ln(B)=0.730\ln(\text{dba})+1.879*\ln(\text{len})-6.206$	0.953	29	0.216	—	0.1-0.6	4.0-80			VF
1	P	$\ln(B)=1.097\ln(\text{cov})+0.331$	0.874	26	0.345	0.2-22	0.1-1.0	15-95		1-2	VF
<i>Lactuca serriola</i> (prickly lettuce)											
2	I	$\ln(B)=0.655*\ln(\text{cov})+1.230$	0.494	14	0.459	0.1-1.5	—	13-75	1		VF
2	I	$\ln(B)=2.072\ln(\text{len})-7.132$	0.861	18	0.178	0.1-1.5	—	13-75	1		VF

Site	age	Type	Equation	R ²	n	MSE	Data range					
							Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/plant	Stem density (no./m ²)	P
<i>Madiá gracilis</i> (slender tarweed)												
1	I		$\ln(B)=0.340\ln(\text{cov})+1.823*\ln(\text{len})-6.090$	0.826	15	0.132	0.6-10	—	34-80		F	
<i>Senecio sylvaticus</i> (wood groundsel)												
1	I		$\ln(B)=1.003\ln(\text{cov})+1.207$	0.973	17	0.090	0.1-32	0.2-1.0	28-85	1-10	F	
1	I		$\ln(B)=0.084*\ln(\text{len})-3.346$	0.809	17	0.632	0.1-32	0.2-1.0	28-85	1-10	F	
1	I		$\ln(B)=1.846*\ln(\text{len})+1.204*\ln(\text{dba})-5.385$	0.963	17	0.140	0.1-32	0.2-1.0	28-85	1-10	F	
2	I		$\ln(B)=1.057*\ln(\text{cov})-0.284$	0.964	22	0.147	0.2-99	0.1-2.1	10-114	—	F	
2	I		$\ln(B)=2.131*\ln(\text{dba})+2.528$	0.875	23	0.555	0.2-99	0.1-2.1	10-114	—	F	
2	I		$\ln(B)=0.061*\ln(\text{len})-3.123$	0.927	23	0.323	0.2-99	0.1-2.1	10-114	—	F	
2	I		$\ln(B)=0.852*\ln(\text{cov})+0.493*\ln(\text{dba})+0.292$	0.972	22	0.121	0.2-99	0.1-2.1	10-114	—	F	
2	I		$\ln(B)=0.761*\ln(\text{cov})+0.019*\ln(\text{len})-1.167$	0.973	22	0.116	0.2-99	0.1-2.1	10-114	—	F	
2	I		$\ln(B)=1.378*\ln(\text{dba})+1.187*\ln(\text{len})-2.821$	0.936	23	0.301	0.2-99	0.1-2.1	10-114	—	F	
2	I		$\ln(B)=0.696\ln(\text{cov})+0.450*\ln(\text{dba})+0.540*\ln(\text{len})-1.735$	0.983	22	0.080	0.2-99	0.1-2.1	10-114	—	F	
1	P		$\ln(B)=0.986\ln(\text{cov})+1.189$	0.974	19	0.087	0.1-32	0.2-1.0	28-85	1-10	1-3	F
2	P		$\ln(B)=1.067\ln(\text{cov})-0.449$	0.986	10	0.111	0.2-99	0.1-2.1	10-114	—	1-8	F
2	P		$\ln(B)=2.44*\ln(\text{mdba})+1.443*\ln(\text{num})+2.415$	0.955	11	0.402	0.2-99	0.1-2.1	10-114	—	1-8	F
2	P		$\ln(B)=2.547*\ln(\text{mlen})+1.055*\ln(\text{num})-8.520$	0.931	11	0.621	0.2-99	0.1-2.1	10-114	—	1-8	F
<i>Senecio jacobaea</i> (tansy ragwort)												
1	I		$\ln(B+1)=1.501\ln(\text{cov}+1)-0.125$	0.914	12	0.114	0.4-22		1.0-20	1	V	
Colonizing Perennial Herbs												
<i>Agrostis</i> species (bentgrass)												
1	P		$\text{sqrt}(B)=1.038\text{sqrt}(\text{cov})+0.718$	0.886	14	0.193	0.3-20		15-60		1-15	VF
<i>Anaphalis margaritacea</i> (pearly everlasting)												
1	I		$\ln(B)=1.023*\ln(\text{len})+1.116*\ln(\text{ns})-2.831$	0.658	14	0.324	0.4-4.0		7.8-33	1-4		VF
1	P		$\ln(B)=1.091\ln(\text{cov})+0.597$	0.877	15	0.132	0.4-7.0		7.8-140	1-4	1	VF
<i>Campanula scouleri</i> (Scouler's harebell)												
1	P		$\ln(B+1)=1.336\ln(\text{cov}+1)+0.119$	0.977	12	0.011	0.1-3.5		—		1-15	VF
<i>Epilobium angustifolium</i> (fireweed)												
1	I		$\ln(B)=1.200*\ln(\text{cov}+1)-0.212$	0.962	26	0.054	0.1-32	—	1.0-77	1-2		V
1	I		$\ln(B)=1.957*\ln(\text{len})-4.850$	0.940	26	0.286	0.1-32	—	1.0-77	1-2		V
1	I		$\ln(B)=0.827\ln(\text{cov}+1)+1.319*\ln(\text{len})-4.267$	0.975	26	0.123	0.1-32	—	1.0-77	1-2		V
2	I		$\ln(B)=1.865*\ln(\text{len})-5.714$	0.884	41	0.441	—	—	2.0-49	1-32		V
2	I		$\ln(B)=1.719\ln(\text{len})+0.451*\ln(\text{ns})-5.576$	0.918	41	0.321	—	—	2.0-49	1-32		V
1	P		$\ln(B)=1.266*\ln(\text{cov})-0.343$	0.949	32	0.241	0.1-72	—	1.0-77	1-2	1-9	V
1	P		$\ln(B)=0.757\ln(\text{cov})+0.986*\ln(\text{mlen}+1)-2.837$	0.963	30	0.158	0.1-32	—	1.0-77	1-2	1-2	V
2	P		$\ln(B+1)=1.143*\ln(\text{cov}+1)-0.008$	0.991	18	0.031	0.1-65	—	2.0-73	1-32	1-24	V

Site	age	Type	Equation	R ²	n	MSE	Data range					
							Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/plant	Stem density (no./m ²)	P
2	P		$\ln(B+1)=1.042\ln(\text{cov}+1)+0.153*\ln(\text{mlen})-0.255$	0.994	18	0.021	0.1-65	—	2.0-73	1-32	1-24	V
2	P		$\ln(B)=1.92*\ln(\text{mlen})+0.902*\ln(\text{num})-5.754$	0.984	18	0.202	0.1-65	—	2.0-73	1-32	1-24	V
<i>Epilobium watsonii</i> (Watson's willow-herb)												
1	I		$\ln(B+1)=1.432\ln(\text{cov}+1)+0.098$	0.886	11	0.132	0.1-8.5	—	12-40	—	—	V
2	I		$\ln(B)=1.839*\ln(\text{len}+1)-7.125$	0.793	110	0.445	—	—	1.0-80	1-5	—	VF
2	I		$\ln(B)=1.760\ln(\text{len}+1)+0.774*\ln(\text{ns})-6.977$	0.806	110	0.422	—	—	1.0-80	1-5	—	VF
<i>Equisetum telmateia</i> (giant horsetail)												
1	P		$\text{sqrt}(B)=1.371\text{sqrt}(\text{cov})-0.109$	0.937	15	0.069	0.2-8.0	—	11-30	—	1-10	V
1	P		$\ln(B)=2.496*\ln(\text{mlen})+1.122*\ln(\text{num})-6.802$	0.823	16	0.321	0.2-8.0	—	11-30	—	1-10	V
<i>Gnaphalium microcephalum</i> (white cudweed)												
1	I		$\text{sqrt}(B)=1.569\text{sqrt}(\text{cov})-0.214$	0.932	18	0.109	0.1-8.0	—	3.0-47	—	—	VF
2	I		$\ln(B+1)=1.536*\ln(\text{cov}+1)+0.072$	0.969	17	0.096	0.1-25	—	1.0-73	—	—	VF
2	I		$\ln(B)=2.152*\ln(\text{len})-5.111$	0.950	17	0.651	0.1-25	—	1.0-73	—	—	VF
2	I		$\ln(B+1)=1.233\ln(\text{cov}+1)+0.253*\ln(\text{len})-0.265$	0.987	17	0.043	0.1-25	—	1.0-73	—	—	VF
<i>Lotus crassifolius</i> (big deervetch)												
2	I		$\ln(B)=2.144*\ln(\text{dba})+2.582$	0.894	22	0.179	—	0.2-1.0	12-76	1	—	V
2	I		$\ln(B)=2.112*\ln(\text{len})-6.542$	0.889	22	0.188	—	0.2-1.0	12-76	1	—	V
2	I		$\ln(B)=1.165\ln(\text{dba})+1.097*\ln(\text{len})-2.096$	0.948	22	0.093	—	0.2-1.0	12-76	1	—	V
1	P		$\ln(B)=0.972\ln(\text{cov})+0.038$	0.986	21	0.041	0.2-70	—	6.1-21	1	1-42	V
2	P		$\ln(B)=1.124\ln(\text{cov})+0.086$	0.986	19	0.071	0.2-100	0.2-1.0	12-70	1	1-16	V
2	P		$\ln(B)=2.483*\ln(\text{mdba})+0.846*\ln(\text{num})+3.005$	0.963	11	0.160	0.2-100	0.2-1.0	12-70	1	1-16	V
2	P		$\ln(B)=2.47*\ln(\text{mlen})+1.084*\ln(\text{num})-7.291$	0.909	19	0.503	0.2-100	0.2-1.0	12-70	1	1-16	V
<i>Lupinus latifolius</i> (broadleaf lupine)												
1	I		$\ln(B)=1.282\ln(\text{cov})+0.318$	0.962	16	0.182	0.1-32	—	3.0-55	—	—	VF
1	I		$\ln(B)=2.294*\ln(\text{len})-5.213$	0.888	16	0.545	0.1-32	—	3.0-55	—	—	VF
2	I		$\ln(B)=1.122\ln(\text{cov})+0.260$	0.969	16	0.196	0.1-90	—	5.0-74	—	—	VF
2	I		$\ln(B)=2.471*\ln(\text{len})-6.498$	0.786	22	1.043	0.1-90	—	5.0-74	—	—	VF
1	P		$\ln(B)=1.230*\ln(\text{cov})+0.287$	0.960	18	0.196	0.1-32	—	3.0-55	—	1-2	VF
1	P		$\ln(B)=0.907\ln(\text{cov})+0.709*\ln(\text{mlen})-1.503$	0.973	18	0.140	0.1-32	—	3.0-55	—	1-2	VF
2	P		$\ln(B+1)=1.193\ln(\text{cov}+1)-0.041$	0.984	21	0.050	0.1-90	—	5.0-74	—	1-8	VF
<i>Lucula campestris</i> (field woodrush)												
1	I		$\ln(B)=1.852\ln(\text{cov})+0.761$	0.981	5	0.069	0.2-1.5	—	3.0-55	—	—	F
<i>Pteridium aquilinum</i> (bracken)												
1	I		$\ln(B)=1.124*\ln(\text{cov})+0.282$	0.837	58	0.287	0.1-9.0	0.1-0.7	5.0-65	—	—	V
1	I		$\ln(B)=2.091*\ln(\text{len})-6.190$	0.866	58	0.236	0.1-9.0	0.1-0.7	5.0-65	—	—	V
1	I		$\ln(B)=0.389\ln(\text{cov})+1.415*\ln(\text{len})-4.121$	0.875	58	0.223	0.1-9.0	0.1-0.7	5.0-65	—	—	V
1	P		$\ln(B)=1.168*\ln(\text{cov})+0.318$	0.882	36	0.285	0.1-15	0.1-0.7	5.0-60	—	1-5	V
1	P		$\ln(B)=2.113\ln(\text{mlen})+0.953*\ln(\text{num})-6.164$	0.900	36	0.249	0.1-15	0.1-0.7	5.0-60	—	1-5	V

Site age	Type	Equation	R ²	n	MSE	Data range					P
						Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/ plant	Stem density (no./m ²)	
Colonizing Tall Shrubs											
<i>Arctostaphylos columbiana</i> (bristly manzanita)											
1	I	$\text{sqr}(B)=1.591*\text{sqr}(\text{cov})-0.261$	0.956	13	0.010	0.2-1.8	0.1-0.4	5.0-19	1	V	
1	I	$\ln(B)=2.421*\ln(\text{dba})+3.506$	0.931	13	0.080	0.2-1.8	0.1-0.4	5.0-19	1	V	
1	I	$\ln(B)=1.398\ln(\text{dba})+$ $1.154*\ln(\text{len})-0.821$	0.963	13	0.047	0.2-1.8	0.1-0.4	5.0-19	1	V	
2	I	$\text{sqr}(B)=2.671\text{sqr}(\text{cov})-1.569$	0.950	11	0.473	2.0-25	0.5-2.1	21-55	1-14	V	
2	I	$\ln(B)=2.025*\ln(\text{dba})+3.527$	0.901	11	0.100	2.0-25	0.5-2.1	21-55	1-14	V	
2	B	$\ln(B+1)=5.389*\ln(\text{bdba}+1)-$ 0.333	0.899	81	0.080	—	0.1-0.9	2.0-50	1-12	V	
2	B	$\ln(B+1)=4.488*\ln(\text{bdba}+1)+$ $0.077*\text{nsb}-0.294$	0.911	73	0.072	—	0.1-0.9	2.0-50	1-12	V	
2	B	$\ln(B)=2.590*\ln(\text{blen}+1)-7.149$	0.909	81	0.276	—	0.1-0.9	2.0-50	1-12	V	
2	B	$\ln(B)=2.281\ln(\text{blen}+1)+$ $0.162*\text{nsb}-6.736$	0.945	73	0.170	—	0.1-0.9	2.0-50	1-12	V	
<i>Ceanothus sanguineus</i> (redstem ceanothus)											
1	I	$\ln(B)=2.875*\ln(\text{dba})+3.134$	0.759	11	0.367	0.1-0.9	0.1-0.3	2.0-21	1	V	
1	I	$\ln(B)=1.888\ln(\text{len})-5.572$	0.946	10	0.091	0.1-0.4	0.1-0.3	2.0-17	1	V	
2	I	$\ln(B)=2.476*\ln(\text{dba})+2.874$	0.823	23	0.466	—	0.1-0.6	3.0-45	1-7	V	
2	I	$\ln(B)=1.878*\ln(\text{len})-5.422$	0.916	23	0.221	—	0.1-0.6	3.0-45	1-7	V	
2	I	$\ln(B)=1.588\ln(\text{len})+$ $0.173*\text{ns}-5.341$	0.947	23	0.146	—	0.1-0.6	3.0-45	1-7	V	
2	P	$\ln(B)=0.917*\ln(\text{cov})+0.235$	0.973	5	0.063	0.2-8.0	0.2-0.4	7.0-30	1-7	1-7 V	
2	P	$\text{sqr}(B)=5.488*\text{sqr}(\text{mdba})+$ $0.274*\text{num}-2.069$	0.994	5	0.013	0.2-8.0	0.2-0.4	7.0-30	1-7	1-7 V	
2	P	$\text{sqr}(B)=0.309\text{sqr}(\text{mlen})+$ $1.159*\text{sqr}(\text{num})-1.471$	0.997	5	0.006	0.2-8.0	0.2-0.4	7.0-30	1-7	1-7 V	
<i>Ceanothus velutinus</i> (snowbrush)											
1	I	$B=1.038\text{cov}-0.088$	0.847	7	0.005	0.1-0.5	0.1-0.2	3.0-11	1	V	
2	I	$\ln(B)=0.879\ln(\text{cov})+0.640$	0.625	19	0.243	0.3-5.0	0.2-0.6	11-43	1	V	
2	I	$\ln(B)=0.054*\ln+0.190*\text{ns}$	0.553	19	0.307	0.3-5.0	0.2-0.6	11-43	1	V	
<i>Ribes lobbii</i> (gummy gooseberry)											
1	I	$\ln(B)=1.261*\ln(\text{cov})+0.330$	0.908	17	0.235	0.1-11	0.1-0.9	4.0-45	1	V	
1	I	$\ln(B)=2.504*\ln(\text{dba})+2.932$	0.877	16	0.253	0.1-4.0	0.1-0.5	4.0-45	1	V	
1	I	$\ln(B)=1.829*\ln(\text{len})-4.867$	0.834	17	0.424	0.1-11	0.1-0.9	4.0-45	1	V	
1	I	$\ln(B)=0.679*\ln(\text{cov})+$ $1.346*\ln(\text{dba})+1.694$	0.960	17	0.111	0.1-11	0.1-0.9	4.0-45	1	V	
1	I	$\ln(B)=0.859*\ln(\text{cov})+$ $0.701*\ln(\text{len})-1.716$	0.939	17	0.168	0.1-11	0.1-0.9	4.0-45	1	V	
1	I	$\ln(B)=1.419\ln(\text{dba})+$ $0.939*\ln(\text{len})-1.032$	0.985	16	0.034	0.1-4.0	0.1-0.5	4.0-45	1	V	
<i>Rubus leucodermis</i> (black raspberry)											
1	I	$\ln(B)=1.285\ln(\text{cov})-0.056$	0.990	11	0.040	0.2-15	0.1-1.1	5.0-85	1	V	
1	I	$\ln(B)=2.334*\ln(\text{dba})+3.012$	0.917	12	0.313	0.2-15	0.1-1.1	5.0-85	1	V	
1	I	$\ln(B)=1.712*\ln(\text{len})-4.452$	0.915	12	0.319	0.2-15	0.1-1.1	5.0-85	1	V	
1	I	$\ln(B)=1.229*\ln(\text{dba})+$ $0.884*\ln(\text{len})-0.802$	0.956	12	0.186	0.2-15	0.1-1.1	5.0-85	1	V	

Site	age	Type	Equation	R ²	n	MSE	Data range				P
							Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/plant	
<i>Rubus parviflorus</i> (thimbleberry)											
1	I		$\ln(B)=2.823\ln(\text{cov}+1)-2.216$	0.917	21	0.114	0.1-3.5	—	5.0-20	—	V
1	I		$\ln(B)=2.298*\ln(\text{len})-5.500$	0.786	21	0.295	0.1-3.5	—	5.0-20	—	V
1	P		$\ln(B)=1.240\ln(\text{cov})+0.044$	0.935	29	0.149	0.1-21	—	5.0-24	—	1-10 V
<i>Sambucus cerulea</i> (blue elderberry)											
1	I		$\text{sqr}(B)=1.248*\text{sqr}(\text{cov})-0.339$	0.942	13	0.011	0.2-2.0	0.2-0.6	3.0-14	1	V
1	I		$\ln(B)=1.274\ln(\text{cov})+0.636*\ln(\text{len})-1.578$	0.953	13	0.086	0.2-2.0	0.2-0.6	3.0-14	1	V
1	I		$\ln(B)=1.891*\ln(\text{dba})+1.218*\ln(\text{len})-1.019$	0.913	13	0.157	0.2-2.0	0.2-0.6	3.0-14	1	V
Forest Herbs											
<i>Galium triflorum</i> (sweetscented bedstraw)											
1	P		$\ln(B)=0.980\ln(\text{cov})-0.602$	0.910	24	0.142	0.1-4.5	—	—	—	1-15 VF
<i>Hieracium albiflorum</i> (white-flowered hawkweed)											
1	P		$\ln(B)=1.222*\ln(\text{cov})+0.559$	0.779	21	0.244	—	—	2.0-110	—	1-6 VF
1	P		$\ln(B)=0.872\ln(\text{cov})+0.309*\ln(\text{mlen})-0.266$	0.905	21	0.111	0.4-7.0	—	2.0-110	—	1-6 VF
<i>Trientalis latifolia</i> (western starflower)											
1	P		$\text{sqr}(B)=0.873\text{sqr}(\text{cov})+0.054$	0.740	14	0.039	0.1-2.4	—	—	—	1-18 V
<i>Viola sempervirens</i> (evergreen violet)											
1	P		$\ln(B)=0.937\ln(\text{cov})+0.583$	0.975	12	0.039	0.1-5.5	—	—	—	1-47 VF
Forest Low Shrubs and Sub-shrubs											
<i>Berberis nervosa</i> (Oregongrape)											
1	P		$\text{sqr}(B)=1.698\text{sqr}(\text{cov})-0.340$	0.980	21	0.051	0.1-11	—	—	—	1-36 V
3	P		$\ln(B)=1.161*\ln(\text{cov})+1.389$	0.937	21	0.212	0.1-30	—	4.5-33	—	1-40 V
3	P		$\ln(B)=0.990\ln(\text{cov})+0.695*\ln(\text{mlen})-0.214$	0.955	21	0.161	0.1-30	—	4.5-33	—	1-40 V
3	P		$\ln(B)=1.546*\text{sqr}(\text{mlen})+0.164*\text{num}-2.764$	0.891	21	1.190	0.1-30	—	4.5-33	—	1.40 V
<i>Gaultheria shallon</i> (salal)											
1	P		$\ln(B)=1.342\ln(\text{cov})+0.483$	0.956	13	0.236	0.1-11	—	—	—	1-61 V
3	P		$\ln(B+1)=1.473*\ln(\text{cov}+1)+0.426$	0.954	19	0.125	0.1-32	—	2.0-40	—	V
3	P		$\ln(B)=1.082\ln(\text{cov})+0.629*\ln(\text{mlen})-0.017$	0.982	19	0.074	0.1-32	—	2.0-40	—	V
<i>Rubus ursinus</i> (Pacific blackberry)											
1	P		$\ln(B+1)=1.068\ln(\text{cov}+1)-0.048$	0.985	13	0.029	0.2-80	—	—	—	1-42 V
3	P		$\ln(B+1)=1.006\ln(\text{cov}+1)+0.386$	0.905	19	0.141	0.3-90	—	—	—	V
<i>Whipplea modesta</i> (whipplevine)											
1	P		$\ln(B)=1.065\ln(\text{cov})+0.513$	0.955	14	0.102	0.2-12	—	—	—	1-34 V
3	P		$\ln(B)=1.053\ln(\text{cov})+1.129$	0.972	17	0.056	0.6-36	—	—	—	V

Site age	Type	Equation	R ²	n	MSE	Data range				
						Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/plant	Stem density (no./m ²)
Forest Tall Shrubs and Understory Hardwood Trees										
<i>Rhododendron macrophyllum</i> (Pacific rhododendron)										
1	I	$\text{sqrt}(B)=6.043*\text{sqrt}(\text{dba})-2.678$	0.699	38	0.187	—	0.2-0.8	3.0-35	1	V
1	I	$\ln(B)=2.219\ln(\text{len})-5.673$	0.947	38	0.126	—	0.2-0.8	3.0-35	1	V
2	I	$\ln(B)=2.640*\ln(\text{dba})+3.413$	0.957	31	0.100	—	0.2-1.1	9.0-63	1	V
2	I	$\ln(B)=2.660*\ln(\text{len})-7.299$	0.964	31	0.083	—	0.2-1.1	9.0-63	1	V
2	I	$\ln(B)=1.237\ln(\text{dba})+1.471*\ln(\text{len})-2.503$	0.981	31	0.044	—	0.2-1.1	9.0-63	1	V
3	I	$\ln(B)=2.541*\ln(\text{dba})+3.130$	0.938	32	0.112	—	0.3-1.7	7.0-90	1	V
3	I	$\ln(B)=0.051*\text{len}+0.146$	0.915	32	0.153	—	0.3-1.7	7.0-90	1	V
3	I	$\ln(B)=1.567\ln(\text{dba})+0.021*\text{len}+1.876$	0.955	32	0.084	—	0.3-1.7	7.0-90	1	V
<i>Castanopsis chrysophylla</i> (golden chinquapin)										
1	I	$\ln(B)=2.397*\ln(\text{dba})+3.289$	0.845	23	0.140	—	0.2-0.6	11-50	1	V
1	I	$\ln(B)=2.397*\ln(\text{dba})+3.289$	0.845	23	0.140	—	0.2-0.6	11-50	1	V
1	I	$\ln(B)=5.411\text{dba}+0.025*\text{len}-1.969$	0.895	23	0.100	—	0.2-0.6	11-50	1	V
Coniferous Tree Seedlings										
<i>Pseudotsuga menziesii</i> (Douglas-fir)										
1	I	$\text{sqrt}(B)=3.701*\text{sqrt}(\text{dba})-0.816$	0.971	11	0.017	0.1-1.0	0.1-0.7	3.0-24	1	V
1	I	$\ln(B)=2.355*\ln(\text{len})-6.030$	0.944	11	0.210	0.1-1.0	0.1-0.7	3.0-24	1	V
1	I	$\ln(B)=0.870\ln(\text{dba})+1.577*\ln(\text{len})-2.903$	0.986	11	0.054	0.1-1.0	0.1-0.7	3.0-24	1	V

^a Site age: number of growing seasons after clearcut logging and slash burning.

^b Equation type: I = individual stem-based equation, P = plot-based equation. A branch-based (B) equation was developed for *Arctostaphylos columbiana* because it branches profusely from a point at the ground surface after the first growing season.

^c Predicted biomass, B, is in units of grams/stem (I equations), grams/m² (P equations), or grams/branch (B equations).

^d Cover (cov): ocular estimate of projected canopy cover (percentage of a 1 m² plot both for individual stem- [I] and plot-based [P] equations).

^e Basal diameter (dba, mdba, bdba): for individual stem-based (I) equations, the diameter (dba) at the ground surface in centimeters; for plot-based (P) equations, the mean diameter (mdba) of all above-ground stems; and for branch-based (B) equations, the diameter (bdba) of the branch at the point where it joins the main axis of the plant.

^f Length (len, mlen, blen): for individual stem-based (I) equations, the length (len) of the primary stem from base to tip in centimeters (if phenology = V) or to the tip of the flower or inflorescence (if phenology = VF or F); for plot-based (P) equations, the modal length (mlen) of all above-ground stems (as above for V, VF, and F); for branch-based (B) equations, the length of the branch (blen) from the point where it joins the main axis of the plant to the tip of the branch.

^g Number of shoots/plant (ns, nsb): number of primary shoots (ns) per above-ground stem; for branch-based (B) equations the number of secondary, or side branches (nsb) per primary branch.

^h Stem density (num): number of above-ground stems per 1 m² plot; for plot-based (P) equations only. Based on point of emergence from the ground surface.

ⁱ P: Phenological state; V = all plants vegetative, VF = some plants in flower and/or fruit, F = all plants in flower and/or fruit.

^j Plants with basal rosettes of leaves only; length is modal leaf length. For *Agoseris grandiflora*, because this equation represents non-flowering plants only, it was not chosen as a primary equation.

^k Sometimes a biennial or short-lived perennial.