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Comparing predictive measures and model functions for estimating plant biomass: lessons from a sagebrush–rabbitbrush community

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Abstract Biologists often use predictive models to estimate plant biomass non-destructively. These models take many forms and employ a variety of predictor measures; however, it is frequently unclear which models produce the most accurate predictions. Here, I asked how model accuracy differed among model functions and predictor measures for estimating plant aboveground biomass and whether there were general trends associated with the amount of variability in the predictor measures. In a sagebrush–rabbitbrush meadow in Colorado, USA, I measured the aboveground biomass and corresponding predictor measures (height, cover, and volume) of 50 forb and shrub species representing 19 plant families. I applied four model functions (simple linear, second-degree polynomial, exponential, and power) to each predictor measure for every species, calculated the accuracy of predicted values using cross-validation, and then compared accuracy across model functions and predictors. I found that choice of predictor measure and model function had an interactive effect on model accuracy. Plant cover and volume were more accurate predictors than height and had high accuracy when fitted with simple linear, polynomial, or power regression, but not an exponential function. Cover and height were more accurate predictors when there was greater variability in these measures. This study indicates that accurate predictive models of forb and shrub biomass can frequently be easily obtained using simple linear regression and cover or volume data. Curvilinear functions can have greater predictive accuracy for some species, but not as many as may be expected based on the prevalence of allometric models in the literature.

Keywords Plant biomass · Non-destructive sampling · Biomass estimation · Model accuracy · Shrubs · Forbs

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Introduction

Plant aboveground biomass is a primary characteristic of terrestrial ecosystems and is measured with a variety of techniques (Chapman 1986; Catchpole and Wheeler 1992). While destructive sampling is

commonly used to measure plant biomass, non-destructive sampling approaches are often preferable because they require less effort and allow for repeated sampling (Chapman 1986; Catchpole and Wheeler 1992). In general, non-destructive sampling is conducted by measuring plant traits that are highly correlated with biomass and that can be used as reliable predictors of biomass in regression models (Chapman 1986; Catchpole and Wheeler 1992). Though these methodologies require some, minimal destructive sampling to calibrate the models, biomass estimation from regressions is non-destructive. Plant biologists have developed many such non-destructive methods, using a wide variety of predictor measures and types of regression models (Catchpole and Wheeler 1992; Rottgermann et al. 2000; Radloff and Mucina 2007; Wallace et al. 2017; Gonzalez de Tanago et al. 2018). These predictive models have mainly been developed for particular species and/or systems and consideration of the comparative accuracy of different methods is often lacking. The number of studies evaluating the relative performance of methods for non-destructively estimating plant biomass is growing quickly (e.g., Gutierrez and Aguilera 1989; Sah et al. 2004; Siebert et al. 2004; Gries et al. 2005; Whitbeck and Grace 2006; Hirata et al. 2007; Ebrahimi et al. 2008; Byrne et al. 2011; Axmanova et al. 2012; Redjadj et al. 2012; Onodi et al. 2017; Pottier and Jabot 2017), but few generalities have emerged to guide those seeking to estimate biomass. Thus, an outstanding question in the estimation of plant biomass is whether there are particular non-destructive methodologies that are reliable across species and systems.

In this study, I evaluated the accuracy of predictive models for the aboveground biomass of 50 forb and shrub species that vary in size and shape. My goal was to assess whether particular methods were preferable across this variability in plant form, focusing on the accuracy of models performed with different predictor measures and with different model functions.

Plant height and cover area are two of the most common metrics used to predict plant biomass (Gutierrez and Aguilera 1989; Rottgermann et al. 2000; Flombaum and Sala 2007; Axmanova et al. 2012; Onodi et al. 2017; Pottier and Jabot 2017), and these measures can be combined to calculate plant volume as a predictor variable (Gutierrez and Whitford 1987; Hirata et al. 2007; Penderis and Kirkman 2014; Grinath et al. 2015). In addition, common functions used to model the relationships between predictor measures and plant biomass include simple linear regression and curvilinear models, such as second-degree polynomial (quadratic), exponential, and power regressions (Gutierrez and Whitford 1987; Gutierrez and Aguilera 1989; Sah et al. 2004; Siebert et al. 2004; Hirata et al. 2007). Although some investigators have simultaneously considered different model functions and predictor measures for estimating biomass within their studies (e.g., Gutierrez and Whitford 1987; Gutierrez and Aguilera 1989; Sah et al. 2004; Pottier and Jabot 2017), little work has explicitly evaluated how model accuracy depends on the concurrent choice of predictor measure and model function (but see Ohsowski et al. 2016). For each species studied here, I conducted twelve models consisting of the factorial combination of four different model functions (simple linear, second-degree polynomial, exponential, and power) and three predictor measures (height, cover, volume) to systematically assess whether dependencies occurred between these methodological factors.

Furthermore, I investigated the potential for general trends in model accuracy associated with the amount of variation in the predictor measures. In particular, I was interested in understanding how the accuracy of models using different predictor variables depended on the ratio of variation in plant cover vs. height. Previous studies in ecology have shown that predictor variables with relatively greater variability have a larger effect on the dependent variable than predictors that are less variable (e.g., Vazquez et al. 2005). Therefore, I expected models based on cover to be most accurate as the relative variability in cover increased and for height-based models to be most accurate when height is highly variable compared to cover. Moreover, I expected the accuracy of models based on plant volume to be consistently high across variability in cover vs. height because volume integrates both of these measurements. Support for these relationships may point the way toward generalizable guidelines for non-destructive estimation of plant biomass.

Methods

Experimental system

This study was conducted in a montane meadow in Almont, Colorado, USA (meadow size = ~ 2 ha, elevation = 2769 m, latitude = 38.719, longitude = − 106.816). The meadow is composed of perennial forbs, shrubs, and grasses, which are primarily active during the short summer growing season and remain dormant over the long, cold winters. Dominant plants include sagebrush (*Artemisia tridentata*) and rabbitbrush (*Chrysothamnus viscidiflorus*), which host herbivorous insects and honeydew-tending ants (*Formica obscuripes*) that have been the focus of previous research at this site (Reithel and Campbell 2008; Erickson et al. 2012; Grinath et al. 2012, 2015; Grinath 2018). The present study focuses on 50 species from 19 plant families, comprising the majority of the forb and shrub assemblage occurring in this meadow (listed in Table 1). Species were identified using Darrow (2006) and the herbarium at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO (~ 30 km NW of the field site). Current accepted nomenclature was checked using the USDA Plants database (accessed June 2018). Three plant taxa (*Lupinus*, *Taraxacum*, and *Wyethia*) were identified to genus because the site occurs in a hybrid zone and species identification was unclear (Cronquist et al. 1989; Darrow 2006; Reithel and Campbell 2008). Another two plant species were identified to genus (*Astragalus*, *Chenopodium*) because keys and matching herbarium specimens were unavailable. Despite species uncertainty, these taxa had consistent characteristics within the field site that made them amenable to biomass estimation in this study. Grasses were not considered in this investigation.

Experimental design

I compared the accuracy of four model functions and three predictive measures that are commonly used to estimate plant biomass. To fit the models, I collected samples of aboveground dry mass for each species, and prior to collection I measured three corresponding characteristics of each sample that were expected to be predictive of biomass: plant height, cover, and volume. Twenty samples were collected per species (except that 40 samples were collected for *C. viscidiflorus*), for a total of 1020 plant samples. Cover (C) was measured using a 1 m^2 quadrat divided into 1 dm^2 cells with string spaced every 10 cm. The quadrat was laid overtop an individual plant and the number of 1 dm^2 cells that were filled by the plant were counted, estimating to the nearest ¼ cell (0.25 dm^2). Some plant species grow in clusters of several adjacent plant stems for which individuals were uncertain and were measured as whole clusters. Height (H) was measured to the nearest 0.5 cm as the distance from the point of contact with the ground surface to the furthest plant part when stretching the plant to maximum length. Volume (V) was calculated in units of dm^3 as the multiplicative interaction between cover and height, using the equation $V = C \times (H/10)$. Note that H was divided by ten in this equation to obtain units in dm. This equation is for the volume of a rectangular prism and is used because cover was measured with a rectangular quadrat, but it is equivalent to that of a cylinder (when considering cover as circular). While there are many additional ways to calculate plant volume, such as that of a cone, these estimates frequently have the same predictive ability as a prism or cylinder because cover and height have the same relative influence in the estimation. Thus, I used the volume of a prism as a generalized measurement of plant volume. To measure plant mass, the aboveground portion of the plant was clipped at ground level, placed in a paper bag, and stored in a freezer to halt decay. After all samples were collected, they were dried at 65 Celsius for 96 h and then weighed to the nearest 0.001 g. On rare occasion, soil was inadvertently collected with the plant material. These samples were not used in analyses out of concern that the biomass measurements were upwardly biased by soil mass, resulting in a total of 1008 samples used in this study (Online Resource 1 and 2). All samples were collected during the flowering period for each species from June through August 2013.

Next, I applied four model functions to predict aboveground biomass for each plant species and predictor measure. I used common regression methods summarized in Table 2, including simple linear, second-degree polynomial, exponential, and power functions. I natural log transformed the data to express exponential and power regressions in linear form

Table 1 List of plant species studied and the overall best model identified for estimating the aboveground biomass (g) of each species

Species	Family	Available predictor measures	Best function and predictor	Coefficients							Range of predictor
				n	*a*	*b*	*c*	SEE	CF	NRMSE	
Achillea millefolium	Asteraceae	CHV	Simple, V	20	− 0.0197	0.5700***	NA	0.1553	NA	0.306	0.075–3.15
Allium acuminatum	Liliaceae	H	Power, H	19	− 7.8855***	1.9089***	NA	0.3220	1.0532	0.540	10–26.5
Amelanchier alnifolia (s)	Rosaceae	CHV	Simple, C	20	− 1.0860***	5.5443***	NA	1.2591	NA	0.312	0.0875–14.4
Androsace septentrionalis	Primulaceae	H	Simple, H	20	− 0.0334*	0.0087***	NA	0.0069	NA	0.639	4.5–16.5
Antennaria parvifolia	Asteraceae	CHV	Polynomial, C	20	− 1.4504***	7.7274***	− 2.2759*	0.9862	NA	0.315	0.25–1.75
Antennaria pulcherrima	Asteraceae	HV	Simple, V	19	− 0.0384**	0.7045***	NA	0.0109	NA	0.393	0.1125–0.9375
Arenaria congesta	Caryophyllaceae	CHV	Simple, C	20	− 0.6386***	3.2417***	NA	0.3227	NA	0.287	0.25–1.25
Artemisia tridentata (s)	Asteraceae	CHV	Simple, V	20	− 0.0705	1.8499***	NA	0.7373	NA	0.309	0.25–6
Astragalus sp.	Fabaceae	CHV	Simple, C	19	− 0.1912**	1.1851***	NA	0.1827	NA	0.370	0.25–1.25
Balsamorhiza sagittata	Asteraceae	CHV	Simple, V	20	− 0.036	0.6202***	NA	0.2960	NA	0.299	0.25–4
Boechera stricta	Brassicaceae	H	Polynomial, H	20	1.3149***	− 0.0488***	0.0007***	0.0007	NA	0.738	16.5–80.5
Calochortus gunnisonii	Liliaceae	H	Simple, H	20	− 0.1071**	0.0135***	NA	0.0148	NA	0.458	8.5–50
Castilleja angustifolia	Scrophulariaceae	CHV	Simple, V	20	− 0.1091	1.6753***	NA	0.3304	NA	0.399	0.2625–1.95
Castilleja linariifolia	Scrophulariaceae	CHV	Simple, V	20	− 0.0394	0.6695***	NA	0.1741	NA	0.241	0.1375–5.3
Chenopodium atrovirens	Chenopodiaceae	CHV	Simple, V	20	− 0.0405***	0.6082***	NA	0.1516	NA	0.427	0.0875–1.6
Chenopodium sp.	Chenopodiaceae	CHV	Simple, V	19	− 0.0801***	0.6341***	NA	0.0203	NA	0.262	0.0875–4.05
Chrysothamnus depressus (s)	Asteraceae	CHV	Power, V	20	1.0102***	1.2789***	NA	0.3508	1.0635	0.233	0.25–3
Chrysothamnus viscidiflorus (s)	Asteraceae	CHV	Polynomial, C	40	− 0.7773***	3.6763***	0.8904***	0.7823	NA	0.284	0.25–4
Clematis hirsutissima	Ranunculaceae	CHV	Simple, V	19	0.0236	0.5499***	NA	0.3194	NA	0.323	0.1875–12.8

Table 1 continued

Species	Family	Available predictor measures	Best function and predictor	Coefficients							Range of predictor
				n	*a*	*b*	*c*	SEE	CF	NRMSE	
Delphinium nuttallianum	Ranunculaceae	H	Exponential, H	20	− 3.8737***	0.0963***	NA	0.3417	1.0601	0.542	4.5–29
Erigeron eatonii	Asteraceae	HV	Simple, V	20	− 0.0763***	0.8400***	NA	0.0139	NA	0.447	0.075–1.075
Erigeron speciosus	Asteraceae	CHV	Simple, C	20	− 0.3167***	1.4488***	NA	0.2312	NA	0.383	0.25–3
Eriogonum racemosum	Polygonaceae	CHV	Simple, V	20	− 0.0322*	0.9389***	NA	0.1995	NA	0.210	0.075–6.15
Eriogonum umbellatum	Polygonaceae	CHV	Simple, C	20	− 0.8823***	4.6150***	NA	1.0896	NA	0.469	0.25–2.5
Galium boreale	Rubiaceae	CHV	Simple, C	19	− 0.1570	1.8043***	NA	0.3328	NA	0.533	0.15–1.8
Geum triflorum	Rosaceae	HV	Simple, V	20	− 0.0955	1.7844***	NA	0.7787	NA	0.718	0.1125–1.2
Helianthella quinquenervis	Asteraceae	CHV	Polynomial, V	20	− 0.0784	0.7528***	− 0.0618***	0.1497	NA	0.218	0.1–6.5
Heuchera parvifolia	Saxifragaceae	CHV	Simple, C	20	− 0.2108*	1.2089***	NA	0.2308	NA	0.499	0.25–1
Lathyrus lanszwertii	Fabaceae	CHV	Exponential, C	19	− 1.5395***	1.5076***	NA	0.1113	1.0062	0.325	0.25–1.5
Linum lewisii	Linaceae	CHV	Power, C	20	− 0.1057	1.7727***	NA	0.2688	1.0368	0.395	0.25–2.5
Lupinus sp.	Fabaceae	CHV	Polynomial, C	20	0.0220	0.3683	0.4349***	0.3552	NA	0.290	0.25–5.5
Machaeranthera canescens	Asteraceae	CHV	Simple, C	19	− 0.2315°	2.1385***	NA	0.4516	NA	0.350	0.25–2.5
Mahonia repens (s)	Berberidaceae	CHV	Power, C	20	0.7931***	1.7032***	NA	0.2737	1.0382	0.382	0.25–1.25
Mertensia oblongifolia	Boraginaceae	CHV	Exponential, C	20	− 1.7452***	0.8566***	NA	0.2486	1.0314	0.489	0.1375–2.8125
Penstemon crandallii	Scrophulariaceae	CHV	Simple, C	20	− 0.7720***	3.9631***	NA	0.5485	NA	0.305	0.25–1
Penstemon strictus	Scrophulariaceae	HV	Power, V	20	0.2081*	0.9151***	NA	0.2323	1.0273	0.433	0.1375–1.525
Phlox multiflora	Polemoniaceae	CHV	Power, V	20	1.2438***	1.1376***	NA	0.2282	1.0264	0.314	0.0875–1.8
Potentilla gracilis	Rosaceae	CHV	Simple, C	19	− 0.1982***	1.1162***	NA	0.2195	NA	0.281	0.25–2.75
Potentilla hippiana	Rosaceae	CHV	Power, C	20	0.0729	1.6867***	NA	0.3105	1.0494	0.278	0.25–3.25
Pulsatilla patens ssp. *multifida*	Ranunculaceae	CHV	Simple, V	20	− 0.0595	0.8336***	NA	0.2285	NA	0.225	0.1625–4.95

Table 1 continued

Species	Family	Available predictor measures	Best function and predictor	Coefficients							Range of predictor
				n	*a*	*b*	*c*	SEE	CF	NRMSE	
Ranunculus ranunculinus	Ranunculaceae	CHV	Power, V	20	− 0.9866***	0.9980***	NA	0.3073	1.0483	0.455	0.125–2.7
Sedum lanceolatum	Crassulaceae	CHV	Simple, C	19	− 0.5543***	3.4555***	NA	0.2935	NA	0.250	0.25–1
Senecio integerrimus	Asteraceae	H	Power, H	20	− 4.5025***	1.2524***	NA	0.3337	1.0573	0.406	3.5–46
Symphoricarpos oreophilus (s)	Caprifoliaceae	CHV	Simple, V	19	− 0.0610*	0.8003***	NA	0.2291	NA	0.185	0.1875–40.2
Symphyotrichum spathulatum	Asteraceae	CHV	Simple, V	19	− 0.0395***	0.7058***	NA	0.1566	NA	0.252	0.075–8.75
Taraxacum officinale	Asteraceae	CHV	Simple, C	20	− 0.1421*	1.0123***	NA	0.1766	NA	0.549	0.25–1
Taraxacum sp.	Asteraceae	CHV	Simple, C	20	− 0.2882	2.7425***	NA	0.3720	NA	0.537	0.25–1
Tragopogon dubius	Asteraceae	CHV	Exponential, V	20	− 1.2555***	0.5859***	NA	0.3974	1.0822	0.424	0.3–3.75
Vicia americana	Fabaceae	CHV	Exponential, V	20	− 2.6049***	0.5956***	NA	0.3172	1.0516	0.262	0.175–4.05
Wyethia sp.	Asteraceae	CHV	Simple, C	20	− 0.4540***	1.6079***	NA	0.3243	NA	0.232	0.25–7

Most species were forbs, but shrubs are indicated with (s). Available and best predictor measures for each species are indicated by *C* cover (dm^2), *H* height (cm), and *V* volume (dm^3). Model function could be simple (linear), polynomial (second-degree), exponential, or power. Model coefficients are shown with ***$P \leq 0.001$, **$0.001 < P \leq 0.010$, *$0.010 < P \leq 0.050$, and °$0.050 < P \leq 0.100$. Correction factors (CF) are provided for exponential and power functions

Table 2 Model functions applied in this study

Function	Formula	Linear regression form
Simple linear	$Y = a + bX$	$Y = a + bX$
Polynomial (2°)	$Y = a + bX + cX2$	$Y = a + bX + cX2$
Exponential	$Y = e^{(a + bX)}$	$\ln Y = a + bX$
Power	$Y = aX^b$	$\ln Y = \ln a + b\ln X$

Symbols for model coefficients match those provided in Table 1

rather than directly applying non-linear regression because the linear forms often better characterize the data, are more easily applied across many species, and have a long history of application in plant biology (Chapman 1986; Catchpole and Wheeler 1992; Niklas 2004; Xiao et al. 2011). I did not set the y-intercept at zero (e.g., Flombaum and Sala 2007) because the shape of the relationship can change close to zero; here the models were focused on the range of variation present in the plant samples. All models were ran using generalized least squares with the 'gls' function (package 'nlme') in R 3.5.2 (R Core Team 2018). This approach was used to obtain regressions that meet the assumption of homoscedasticity, because heteroscedasticity was problematic even after natural log transformation for some species. For each regression, I used AIC-based selection to determine the optimal variance structure (Zuur et al. 2009). The regression without variance structure was compared with those with three structures (fixed, power, exponential) using AICc to account for small sample sizes (package 'AICcmodavg'). Regressions with variance structure better met the assumption of homoscedasticity if the AICc score was > 2 units lower than that of the base model without structure. If multiple models with variance structure passed this criterion, then the one with the lowest AICc was chosen as optimal. R code for this procedure is included in Online Resource 3.

Of the 50 species studied, 40 had adequate data for each predictor measure to run a total of 12 regressions per species. Six species had no variation in cover ($C = 0.25$ dm^2) and only height was used as a predictor in the regressions; another four species had little variation in cover ($C = 0.25$ or 0.5 dm^2) and both height and volume were used as predictor variables in the regressions. The available predictor measures for each species are listed in Table 1. In total, I performed 536 regressions to compare the accuracy of those using different predictor measures and model functions (listed in Online Resource 4).

For each regression, I used leave-one-out cross-validation (LOOCV) to generate predictions and estimate model accuracy (R code in Online Resource 3). Using an iterative procedure, a single data point was removed and the model re-ran to predict the missing point. The missing datum was replaced before removing the next data point. Biomass data were natural log transformed to conduct the exponential and power regressions and fitted values calculated by back-transformation required correcting because they are biased estimates (Chapman 1986; Catchpole and Wheeler 1992; Niklas 2004; Packard et al. 2011; Xiao et al. 2011). To obtain unbiased values, I applied a correction factor (CF) based on the standard error of the estimate (SEE) for each regression, given by $CF = e^{(SEE2/2)}$ (Sprugel 1983; Strimbu et al. 2018). Estimates from the regressions were multiplied by their corresponding CF to measure unbiased predictions. The accuracy of the predictions was determined using normalized root mean square error (NRMSE) with the 'nrmse' function (package 'hydroGOF'). The root mean square error (RMSE) indicates greater accuracy as it approaches zero; here, these values were normalized by the standard deviation of the observations to obtain values that can be compared across the separate datasets corresponding to each species. I chose NRMSE rather than other metrics, such as the coefficient of determination (R2), because it allows comparison across datasets and types of model functions (Sileshi 2014; Poorter et al. 2015; Pottier and Jabot 2017). NRMSE is commonly applied across the biological and environmental sciences and is becoming more frequently used in the study of plants (e.g., Zhou et al. 2003; Stramski et al. 2008; Shin et al. 2012; Wang et al. 2012; Bai et al. 2014; Shiogama et al. 2016; Pottier and Jabot 2017; Yin et al. 2017).

Statistical analyses

I used linear mixed effects modeling (LMM) to analyze how model accuracy (NRMSE) responded to the type of predictor measure and function (Zuur et al. 2009). The R function 'lme' (package 'nlme') was

used to perform the LMM with species identity included as a random factor to account for the repeated measures for each species. The fixed model structure consisted of the type of predictor measure (3-level factor), type of function (4-level factor), and their interaction. Because variances were unequal across treatment groups, I applied an AIC-based selection procedure to find the optimal variance structure, similar to the above (Zuur et al. 2009). I compared AIC values for models with no variance structure, assuming unequal variances across the model function variable, unequal variances across the predictor measure variable, and unequal variances across groups for the interaction between model function and predictor variable. The model assuming unequal variances for the interaction between variables had the best fit (lowest AIC) and I calculated results for this model using Type III Sum of Squares ('Anova' function from the 'car' package) to account for unequal sample sizes among groups. I considered $P \leq 0.05$ to be statistically significant. Tukey post hoc contrasts were used to assess differences between groups ('glht' function from the 'multcomp' package), using an $\alpha = 0.10$ for clear interpretation of the contrasts. Prior to analysis, observations with extremely low accuracy (NRMSE > 5) were removed from the dataset in order to conduct the LMM. The LMM was validated by visually inspecting the residuals. Though some skew in the residuals was present, LN transformation did not alter the interpretation of the results. Therefore, I present the model based on the complete, untransformed dataset, which can be considered robust to any non-normality in the residuals. The LMM was performed twice to assess whether the availability of predictor measures influenced the results: once with all 50 species and once with the 40 species for which all predictors were available.

I determined the best models by comparing accuracy among the twelve models for each species. For each predictor measure for a given species, the model with the lowest NRMSE value was considered best for that type of predictor. The best overall model had the lowest NRMSE value for that species, regardless of predictor measure. Because polynomial models always have at least as good of fit to the data as simple linear models, polynomial models were only considered during this procedure if the coefficient for the quadratic term was significant (Online Resource 4). I performed a contingency table analysis to determine if there was an association between the frequency of best models found for each type of model function and the type of predictor measure. An additional contingency table analysis was conducted to assess the frequency of best overall models across the types of model functions and the available predictor measures. These associations were evaluated using Fisher's exact test (function 'fisher.test') because too few data existed to use a χ^2 test.

Subsequently, I evaluated whether the accuracy of the best models was associated with the amount of variation in the predictor measures. I measured the coefficient of variation (CV) for the cover and height of each species and then calculated the ratio of CV-cover to CV-height. A value of one would indicate that the variation in cover and height are equal for that species, whereas ratio values less than one indicate greater variation in height and those greater than one have greater variation in cover. I expected that best models using height as a predictor would have greatest accuracy (lowest NRMSE) at low ratio values and be less accurate as the ratio increased. Oppositely, I expected best models using cover as a predictor to have greatest accuracy at high ratio values and lower accuracy as the ratio decreased. I did not consider the CV for plant volume because this predictor measure was calculated from the cover and height data. Because volume integrates the variation in both cover and height, I expected that the accuracy of best models using volume as a predictor would change little with CV-cover:CV-height. To assess these trends, I performed regressions evaluating the accuracy of best models as a function of the CV-cover:CV-height ratio. Separate gls regressions were performed for each predictor measure (height, cover, and volume). Similar to the procedure described above, I considered simple linear, polynomial, exponential, and power functions. Multiple variance structures were considered, as above, but the addition of variance structure was not required to meet the assumption of homoscedasticity. A power function was chosen as best to describe these relationships, based on NRMSE values and inspection of the residuals.

Lastly, I considered whether there were differences in the results between forb and shrub species, focusing on the 40 species that had variability in all three predictor measures. I compared the NRMSE values for the best overall models for forb ($n = 34$) and shrub ($n = 6$) species, as well as the ratio of CV-cover:CV-

height across plant forms. These comparisons were made using gls models with plant form (forb vs. shrub) included as a binary factor. I also considered whether to account for unequal variances between these groups using the same methodology described above. Following these tests, I performed contingency table analyses to determine if there was an association between plant form and the frequency with which predictor measures and model functions were used in the best models. These associations were assessed in separate contingency tables using the same methods as above. All analyses were conducted in R and considered statistically significant if $P \leq 0.05$.

Results

Of the 536 models considered, 19 had very poor accuracy (NRMSE > 5) according to predictions from the cross-validation procedure (Online Resource 4). These extremely inaccurate models primarily used an exponential function with plant height as the predictor (14 models), but were occasionally found using an exponential function with cover (2 models) or volume (1 model) predictor measures, and when using a power function with height (1 model) or volume (1 model) as predictors. Such inaccurate models were not found when using simple linear or polynomial functions.

Excluding the highly inaccurate models (NRMSE > 5), linear mixed effects analysis showed that model accuracy depended on both the predictor measure and the type of function used for the regression (Online Resource 5). Considering all 50 species, there was a significant statistical interaction between predictor measure and model function ($\chi^2 = 14.287$, $P = 0.027$), indicating that different functions attained higher accuracy (lower NRMSE values) for particular predictor measures (Fig. 1). This statistical interaction was also evident when restricting the analysis to the subset of 40 species for which all three predictor measures were available ($\chi^2 = 20.342$, $P = 0.002$); thus, this result is little influenced by species that lacked accuracy values for cover or volume predictors (Online Resource 5). Post hoc contrasts (Fig. 1) revealed that the models using an exponential function were least accurate overall and within each predictor measure. Intermediate accuracy was found for models using simple linear, polynomial, and power functions with plant height as the predictor. The models with greatest accuracy used simple linear, polynomial, and power functions with cover and volume predictor measures; differences in accuracy among these types of models were indistinguishable in the post hoc analysis (Fig. 1).

The distribution of best models across types of predictor measures and functions is summarized in Table 3 and details of the overall best models for each species are provided in Table 1. For all three predictor measures, simple linear regressions were most frequently identified as best models, followed by models with power and polynomial functions, and lastly exponential models (Table 3a). This finding is supported by contingency table analysis, which indicated that the frequency of best models across types of functions was similar for all predictor measures ($P = 0.898$). Considering all three predictor measures together, simple linear functions were the best overall type of model for 31 species (Table 3b). The next most frequent function used in the overall best models was a power function. Polynomial and exponential models were least frequently identified as best overall. Of the 40 species for which all three predictor measures were available, overall best models were based on cover data for 22 species and on volume data for 18 species (Table 1). There was no evidence that the frequency of best models across types of functions was associated with the availability of predictor measures (Table 3b), according to contingency table analysis ($P = 0.578$).

The accuracy of best models across variation in plant cover and height is depicted in Fig. 2 (Online Resource 5). For models using height as the predictor, a significant trendline indicates that greater accuracy was found for plants with low CV-cover:CV-height ratios ($b = 0.229$, $t = 2.455$, $P = 0.018$). In contrast, models using plant cover as the predictor measure were more accurate at higher CV-cover:CV-height ratios ($b = -0.555$, $t = -2.214$, $P = 0.033$). The two species with the least accurate cover-based regressions had CV-cover:CV-height ratios close to one (Fig. 2). The trendline for volume as the predictor measure was similar to that of plant cover, but had a non-significant slope ($b = -0.410$, $t = -1.670$, $P = 0.102$).

There was no evidence that the results depended on whether the plant species were forbs or shrubs. The accuracy of the overall best models ($\chi^2 = 2.060$, $P = 0.151$) and CV-cover:CV-height ratios ($\chi^2 = 0.214$, $P = 0.644$) were not significantly different between forb and shrub plant forms. Also,

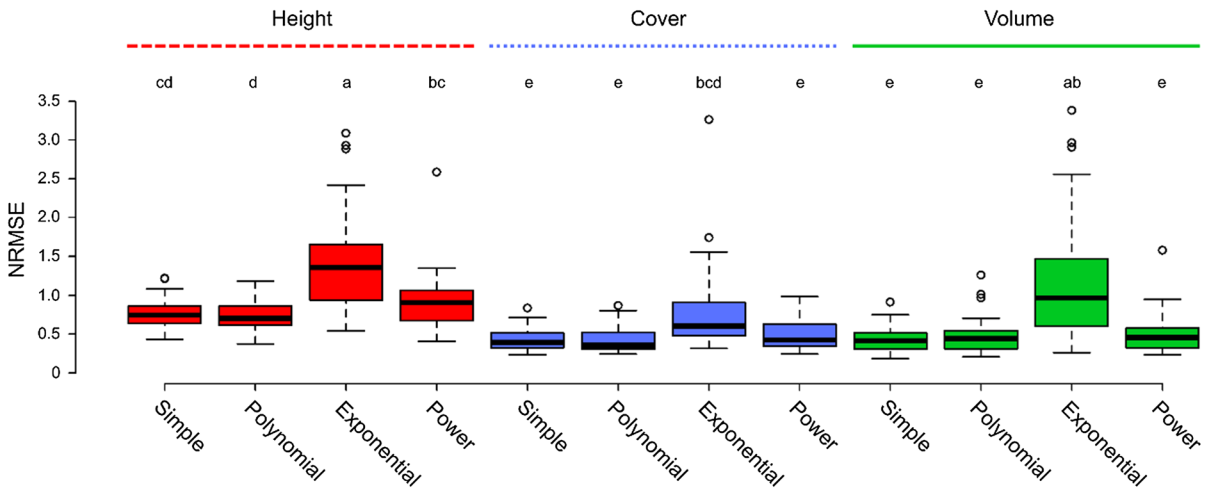

Fig. 1 Accuracy of models across types of predictor measures and functions. Model accuracy was measured as the normalized root mean square error (NRMSE: lower values have greater accuracy) for each of 517 models from 50 plant species. The NRMSE values are shown as boxplots for each group of models. Letters above boxplots indicate Tukey post hoc contrasts using $\alpha = 0.10$

Table 3 Frequencies of best models identified for each type of predictor measure and function

(a) Best models within each predictor measure

	Predictor measure		
	Cover (C)	Height (H)	Volume (V)
Function			
Simple	25	33	32
Polynomial	6	8	4
Exponential	2	1	2
Power	7	8	6
Total species	40	50	44

(b) Best models over all predictor measures

	Available predictor measures			Function total
	CHV	HV	H	
Function				
Simple	26	3	2	31
Polynomial	4	0	1	5
Exponential	4	0	1	5
Power	6	1	2	9
Total species	40	4	6	50

In (a), frequencies of the best model function for each predictor measure are provided. In (b), frequencies of the overall best model function are shown corresponding to the predictor measures that were available for the species

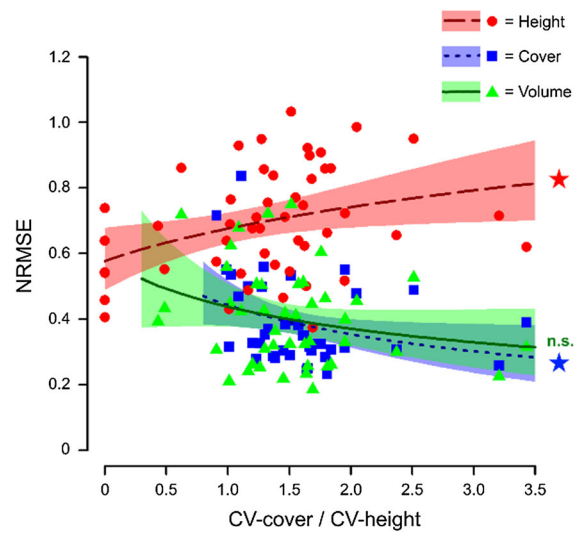

Fig. 2 Accuracy (NRMSE: lower values have greater accuracy) of best-fitting models for each predictor measure across the ratio of variation in cover vs. height. This ratio was measured as the coefficient of variation in cover (CV-cover) divided by that of height (CV-height). Separate power regressions were fit for best models corresponding to each predictor measure. The regressions are shown with 95% confidence intervals and significant slopes ($P \leq 0.05$) are indicated by stars (with matching colors) to the right of the graph

contingency table analyses found that there was no association between plant form and the frequency of best models using plant cover and volume as predictors ($P = 1.000$), nor between plant form and the frequency of best models that used simple linear, polynomial, exponential, or power functions ($P = 0.327$).

Discussion

Despite the variability in species sizes, shapes, and woodiness included here, this study shows that biomass estimates can be easily and reliably found with simple linear regression and cover data. Considering volume as a predictor provided little improvement to prediction accuracy compared to using cover data; thus, the additional work required to measure volume (i.e., collecting height data) may not be necessary. These results support previous research showing that forb and shrub biomass can be accurately estimated from cover data using simple linear regression, and these relationships may also extend to grasses and other plant forms (Rottgermann et al. 2000; Guevara et al. 2002; Siebert et al. 2004; Flombaum and Sala 2007), which deserves additional study. Furthermore, this study provides a clear demonstration of the dependence between choice of predictor measure and model function for obtaining accurate predictions of plant biomass. While simple linear regressions performed with cover or volume provided the best biomass estimates in the majority of cases, the accuracy of estimates could sometimes be enhanced by considering curvilinear functions. Height alone was a poor predictor of biomass, but in particular circumstances, using height to calculate volume can improve biomass estimates.

The calculation of volume data from cover and height tended to improve model accuracy over that of cover-based models only when the amount of variability in cover and height was similar. This result conforms to the expectations that cover-based models would become less accurate when the ratio of variation between cover and height was low, but that the accuracy of volume-based models would change little. This suggests that volume may be the preferable predictor across the range of variation in cover vs. height, but this needs to be weighed against the ease of estimation of plant cover alone. Height was never a preferable predictor measure compared with cover and volume. However, height-based models were more accurate when the ratio of variability in cover vs. height was low, as anticipated. Similar to other relationships (e.g., Vazquez et al. 2005), the relative influence of different predictors on a dependent variable will be contingent on the amount of variability in these measures, with the most variable measure frequently having the greatest impact. Regardless of which predictor measure is chosen for biomass estimation, the predictor must have a large amount of variation reflective of biomass to achieve accurate estimates.

Deciding which model function to use for predicting plant biomass can be difficult, and it may be worth considering multiple options. While choosing between a linear and curvilinear function may be visually assessed fairly easily, choosing among curvilinear approaches is less intuitive. Among curvilinear functions, the results suggest that power, polynomial, and exponential functions are all appropriate options to pursue, though exponential regressions are more likely to provide highly inaccurate predictions. Many studies have focused on applying power or exponential functions without also considering simple linear functions or other types of curvilinear functions (e.g., Johnson et al. 1988; Nafus et al. 2009; Penderis and Kirkman 2014; Berner et al. 2015; Matula et al. 2015; Rojo et al. 2017; He et al. 2018). However, the majority of the species studied here ($n = 31$) had best overall models that were fit with simple linear regression, suggesting that more attention should be given to these straightforward relationships. Moreover, polynomial and exponential functions were identified as best overall models with equal frequency, and power functions were preferred with only slightly greater frequency. Altogether, these results indicate that practitioners should consider several competing models based on simple linear and multiple curvilinear functions (similar to Sah et al. 2004; Siebert et al. 2004; Gries et al. 2005; Hirata et al. 2007), and that power functions may not provide the best estimates as frequently as might be thought. Allometric equations (i.e., power functions) are often published for use in plant biomass estimation, especially in forestry (e.g., Berner et al. 2015; Matula et al. 2015; He et al. 2018; Strimbu et al. 2018). While using published allometric equations requires little effort, those wishing to estimate biomass with such equations should be aware

that other types of regressions may have greater predictive accuracy and check that authors have considered multiple options.

Aboveground biomass of sagebrush and rabbitbrush, the dominant plants included in this investigation, have been estimated by non-destructive methods in previous studies. Several studies found that power functions could accurately estimate sagebrush and rabbitbrush biomass from plant volume data (Tausch 1989; Tausch et al. 1992; Reiner et al. 2010), but other types of curvilinear functions were not considered. In other studies, sagebrush and rabbitbrush volume have been shown to vary linearly with aboveground biomass (Uresk et al. 1977; Grinath et al. 2015), but these studies did not consider competing curvilinear functions. The present study found that a simple linear regression based on volume data was most accurate for predicting sagebrush biomass, supporting previous work (Uresk et al. 1977). Yet, this study also found that a cover-based model fit with a second-degree polynomial function provided the most accurate estimates of rabbitbrush aboveground biomass. These results suggest that previous studies may have found models with greater accuracy had they considered additional model functions and predictors (e.g., Ohsowski et al. 2016). Sagebrush and rabbitbrush are dominant plants throughout western North America (Tilley et al. 2006; Tilley and St. John 2012) and are important contributors to primary production and carbon sequestration. To clarify the role of these plants for ecosystem functioning, further work must be conducted to elucidate which non-destructive methods best estimate the biomass of sagebrush and rabbitbrush.

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