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Quantifying aboveground biomass for common shrubs in northeastern California using nonlinear mixed effect models

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ABSTRACT

Quantifying shrub biomass can assist in natural resource management decision making. Nonlinear mixed effect models (NMEM) were developed to predict total aboveground biomass as well as biomass in leaves, 1-h, 10-h, and 100 or more hour fuel classes for seven species of shrubs common to the northeastern California. Using crown area as a predictor, an allometric (power) model was used as a base model. Coefficients varied by species, component, and by a nested combination of these random effects.

The results showed that NMEM that used shrub species as random effect performed better than nonlinear fixed effect models in estimating total and component biomass in shrub species used in this study. Additionally, when fixed effect models were fitted by species, not all regression parameters were statistically significant at 0.05 level of significance. NMEM were able to account for within species variation very well. The largest variation was observed in total biomass while the smallest variation was observed in the biomass in 100 or more hour fuel class. The mean prediction bias and root mean square prediction errors for total shrub biomass was 0.0409 kg and 0.9249 kg respectively. While there were differences between the fixed effects models and mixed effects models, the mixed effects models would be preferred to the fixed effect models for future studies involving total biomass prediction for similar shrub species and regions.

1. Introduction

Shrubs are important drivers of forest ecosystem productivity and diversity. Forest understory vegetation are ecologically important because shrubs, lichens, and mosses can have a direct effect on belowground processes such as decomposition, nutrient flow, and the accumulation of soil nutrients (Nilsson and Wardle, 2005). A majority of the studies concerning forest biomass assessment by the use of allometric equations has focused solely on the estimation of tree biomass (Beedlow et al., 2009). Although tree biomass is the principle sink of carbon sequestration in forests, it is also necessary to account for shrub biomass, as these woody plants play an active role in ecosystem productivity (Beedlow et al., 2009). A more comprehensive assessment of total biomass will provide land managers and researchers with reliable assessments of site productivity, fuel loading, and treatment effects (Návar et al., 2004).

There have been several studies involving the estimation of shrub biomass for various aspects of forest management including fire risk management (Botequim et al., 2015, Roussopoulos and Loomis, 1979, Sağlam et al., 2008), carbon sequestration (Pasalodos-Tato et al., 2014), ecological stresses or disturbances (Elzein et al., 2011), and wildlife habitat assessment (Grigal and Ohmann, 1977). Shrub biomass has also been estimated using airborne LiDAR in small forest stands (Estomell et al., 2011) and by using satellite remote sensing data to quantify tree and shrub biomass in natural forest stands (Roy and Ravan, 1996).

The primary objective of this study was to develop predictive equations using NMEM for shrubs common to Lassen National Forest, CA. Equations were developed for aboveground biomass of seven species of shrubs using metrics that are easily obtained in the field (Huff et al. 2017). In this study, model performance and different strategies using NMEM were also examined. The random effect coefficients obtained from this research may be applied to shrubs found in other national forests or for when the shrub species is unknown.

Mixed effects models have been used extensively in forestry and in agricultural research. Gregoire and Schabenberger (1996) applied NMEM to predict cumulative bole volume of standing trees. NMEM have been used to incorporate topographic factors with aboveground biomass of Simao pine (*Pinus kesiya* var. *langbianensis*) while utilizing single and nested random effects (Ou, et al., 2016). Variable exponent taper models were developed for three central Oregon tree species using

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NMEM (Garber and Maguire, 2003, Poudel et al. 2018). The use of NMEM has also been found to improve the accuracy and precision of height prediction strategies in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco.) forests (Temesgen et al., 2008). Small numbers of groups (12 counties in Iowa) were successfully used as random effects in a linear mixed effects model for the prediction of county crop areas using survey and satellite data (Battese et al., 1988). NMEM are valuable tools used for growth and yield modeling in forestry disciplines and the use of such models proved to be efficient and reliable within the context of this study.

This study provides equations that predict aboveground biomass for the following seven species of shrubs: mountain whitethorn (*Ceanothus cordulatus* [Kellogg]), snowbrush (*Ceanothus velutinus* [Dougl. ex Hook.]), deerbrush (*Ceanothus integerrimus* [Hook. and Arn.]), bush chinkapin (*Castanopsis sempervirens* [Kellogg]), greenleaf manzanita (*Arctostaphylos patula* [Greene]), golden currant/gooseberry (*Ribes* spp. [Pursh]), and serviceberry (*Amalanchier alnifolia* [Nutt.]). *Ribes* spp. include combined observations of golden currant (*Ribes aureum*) and Sierra gooseberry (*Ribes roezlli*). Predictions derived from this study may be applied to forests in northeastern California where these shrub species are present. Observations with crown area less than 5 m^2 were used in the model fitting process.

2. Materials and methods

2.1. Study area

The study area is located in Lassen National Forest, CA (40°50′N, 121°00′W), which is managed by the United States Forest Service (USFS). The map in Fig. 1 depicts the location of the study area. Elevation ranges from 1700 m to 2100 m for where shrubs were sampled. The annual precipitation varies from 584 mm to 1092 mm with a mean of 1041 mm. A majority of the precipitation comes in the form of snowfall between the months of November to April. The mean annual temperature is 7.2 °C, with a mean temperature of −6.7 °C in January and a mean temperature of 26.7 °C in August. Soils are classified as Typic Argixerolls and Typic Haploxerands, which were formed over colluvium, glacial till, or glacial outwash. Blacks Mountain Experimental Forest, located within Lassen National Forest, is classified as Interior Ponderosa Pine forest cover type (SAF 237) covering 3715 ha (9200 acres) and is the only forest cover type located on the Experimental Forest (Eyre, 1980). Forest composition does vary within this cover type as white fir (*Abies concolor* var. lowiana [Gord.] Lemm.) and incense-cedar (*Libocedrus decurrens* Torr.) become more prevalent at increasing elevations. Lower elevations of Blacks Mountain Experimental Forest consist of poorly drained flats dominated by sagebrush and grass (Adams et al., 2008). Common plant associations within Lassen National Forest include the Jeffery pine (*Pinus jefferyi* [Grev. & Balf.]) /white fir/greenleaf manzanita/snowbrush communities and the California red fir (*Abies magnifica* [A. Murr.]) /white fir/bush chinkapin communities (found in higher elevations) (USDA, 2011).

The historic fire return interval for white fir/greenleaf manzanita/snowbrush plant association is between 8 and 20 years (USDA, 2011). Fire size and intensity influence the presence of shrubs like greenleaf manzanita and snowbrush in areas where these plant associations occur. Greenleaf manzanita and snowbrush seeds may lay dormant in the soil for hundreds of years before fire initiates germination. High severity fires that burn the forest canopy and kill overstory trees allow for shrub communities to thrive in the new openings (USDA, 2011). Fire severity and intensity are important factors in disturbance, especially concerning the establishment of shrubs like greenleaf manzanita, whose seedlings thrive in large numbers during the spring of the postfire year.

2.2. Data

Sampling occurred over the summers of 2011–2013 and a total of 180 individual shrubs were sampled to fill a range of four height classes (0.1–0.5 m, 0.5–1.0 m, 1.0–1.5 m, and 1.5–2.0 m). A minimum of five shrubs per species within each height class was desired. Crews determined if the shrub was free to grow or not. Free to grow, for this study, was defined as whether or not the shrub crown was encroached by neighboring plants. Shrubs were only sampled if the crown dimensions could be readily observed due to the difficulty in measuring such dimensions without damaging the sample. If a tree or snag had fallen across a shrub, it was not selected for sampling. Table 1 lists the shrub species sampled by common and scientific name, abbreviation, and total number of samples obtained for each shrub.

Shrubs were destructively sampled within the area of where the Storrie Fire of 2000 occurred, but not exclusively. In some instances, shrub species within the desired size classes were unable to be located, so samples from Blacks Mountain and Swain Mountain Experimental Forests (located within Lassen National Forest) were used. Ecological knowledge and vegetation maps of the region were used to locate shrubs within this area. Field crews used a random number table to determine and set an arbitrary bearing and then walked that direction until a shrub that had the desired specifications (species; height within a specified height class) was located. Once a shrub with the desired specifications was located, its location was noted using handheld GPS devices, which allows for location precision to within 10 to 20 feet. A measure of crown width (cm) long (a measure of the horizontal crown width axis) and crown width short (a horizontal crown width perpendicular to the crown width long measurement) were obtained. Three measurements of height (cm) were then taken for the tallest, second, and third tallest stems. Three measurements of the largest, second, and third largest basal diameters (cm) were also obtained at 10 cm aboveground and a count for the total number of stems was calculated. A total of eleven measurements were taken on each individual shrub. Table 2 lists the measurements in the order they were obtained in the field along with abbreviations and measurement precision.

Plant material was bagged by size class. Size classes used were adopted from the National Fire Danger Rating (NFDR) fuel classification system. Size classes include leaf (foliage), 1-h fuels (wood < 0.64 cm in diameter), 10-h fuels (wood 0.64–2.54 cm in diameter), 100-h fuels (wood 2.54 – 7.62 cm in diameter), and 1000-h fuels (wood > 7.62 cm in diameter) (Bradshaw et al., 1983). Total biomass is comprised of 1-h, 10-h, 100-h, 1000-h, and leaf biomass components (kg). Wood and leaves were bagged by size class and labeled denoting species, date, and size class of the material. Samples were stored in a dry room until the fall, when oven drying of the samples occurred.

Plant material was oven dried at 80 °C until weight was stabilized (generally 2–3 days). Weight of the leaves and 1-h biomass was processed first. Oven-dry biomass (g) for leaf biomass, 1-h, 10-h, 100-h, and 1000-h fuels were recorded. It should be noted that there was no plant material that was greater than 22.4 cm in diameter and very little of the recorded biomass fell into the 1000-h fuel class.

2.3. Data analysis

Data was organized into three separate categories: shrub measurements obtained in the field, shrub field weights (weights of biomass size classes obtained in the field (g)), and shrub lab weights (weights of biomass size classes after oven drying). Serviceberry had the greatest value for mean height (77.8 cm) with a minimum height of 10 cm and a maximum height of 200 cm. Greenleaf manzanita possessed the largest mean basal diameter (2.1 cm) with a minimum basal diameter of 0.5 cm and a maximum basal diameter of 6.7 cm. Snowbrush had the greatest mean value of crown area (1.3 m^2) with a minimum crown area equal to 0.1 m^2 and a maximum crown area equal to 4.5 m^2. Mountain whitethorn possessed the largest mean total biomass (1.8 kg) with minimum and maximum weights equal to 0.1 kg and 21.7 kg, respectively. Deer brush had the lowest mean total biomass (0.5 kg) with minimum and maximum weights equal to 0.1 kg and 8.5 kg,

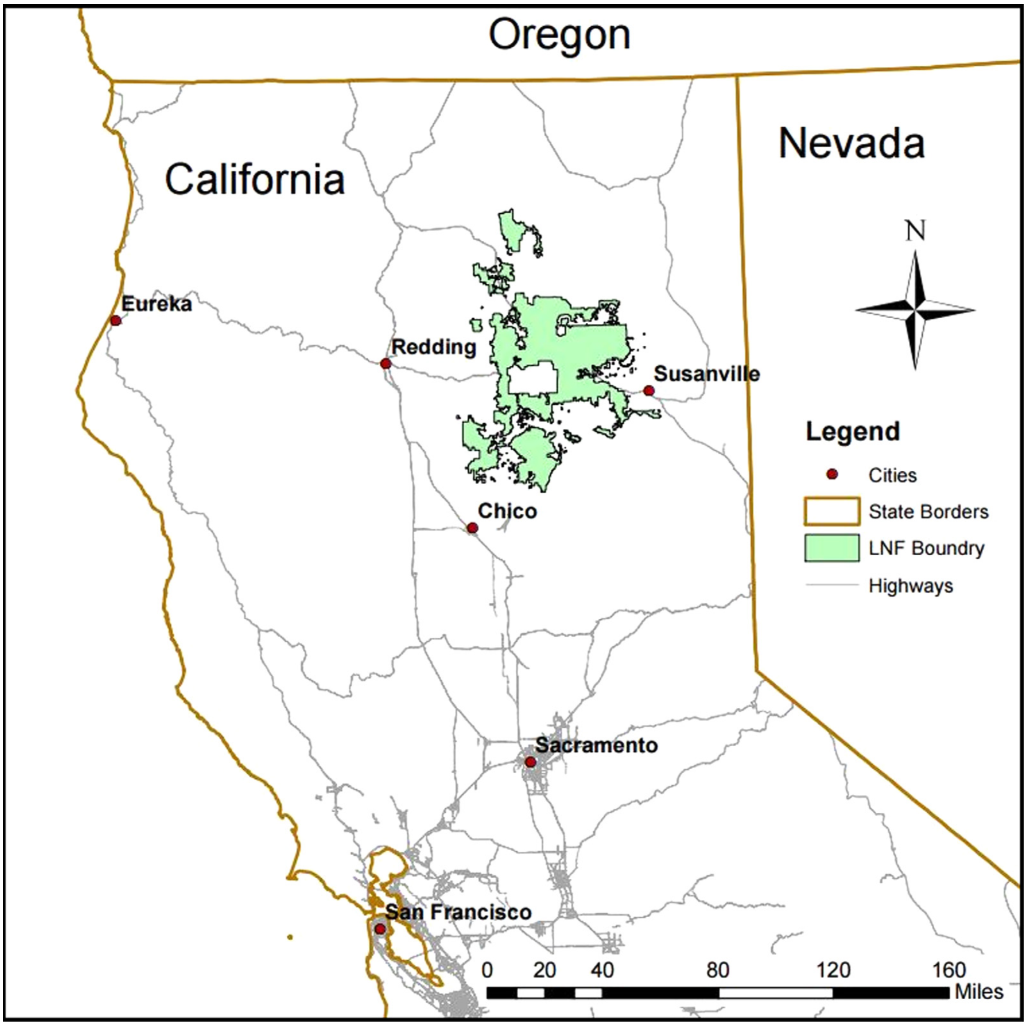

Fig. 1. Map depicting the study area located in Lassen National Forest, CA. Map courtesy of Dr. Martin Ritchie, Pacific Southwest Research Station, U.S. Department of Agriculture.

Table 1
Common and scientific names, abbreviations, and total number of shrub samples.

Species (common)	Species (scientific)	Abbreviation	n
Serviceberry	*Amalanchier alnifolia*	AMAL	28
Greenleaf manzanita	*Arctostaphylos patula*	ARPA	32
Bush chinkapin	*Castanopsis sempervirens*	CASE	20
Mountain whitethorn	*Ceanothus cordulatus*	CECO	27
Deerbrush	*Ceanothus integerrimus*	CEIN	21
Snowbrush	*Ceanothus velutinus*	CEVE	26
Ribes spp. (currant and gooseberry)	*Ribes* spp.	RISP	26

respectively. Summary statistics for shrub height, crown area, and stem diameter at 10 cm aboveground are shown in Table 3.

Crown area was considered as a predictor of shrub biomass due to accurate results obtained in past studies involving the estimation of shrub biomass (McGinnis et al., 2010, Zeng et al., 2010, Maraseni et al., 2005). The calculation of crown area requires two perpendicular measurements of crown width (crown width long (*cwl*, cm) and crown width short (*cws*, cm)), both of which were acquired with field measurements. Crown area (m^2) in this study is defined as the area of a vertical projection of the crown to a horizontal plane (Uzoh and Ritchie, 1996) and calculated as

Table 2
Description and order of the measurements obtained in the field for individual shrubs.

Order	Abbreviation	Description	Desired Precision
1	CWL	Horizontal crown width long axis (cm)	1 cm
2	CWS	Horizontal crown width perpendicular to CWL (cm)	1 cm
3	HM	Maximum vertical height (cm)	1 cm
4	H1	A representative vertical height (cm)	1 cm
5	H2	A representative vertical height (cm)	1 cm
6	H3	A representative vertical height (cm)	1 cm
7	ML	Maximum stem length (cm)	1 cm
8	SC	Stem count at 10 cm	NA
9	D1	Basal diameter at 10 cm (largest)	0.01 cm
10	D2	Basal diameter at 10 cm (second largest)	0.01 cm
11	D3	Basal diameter at 10 cm (third largest)	0.01 cm

$$ca = cwl \times cws \times \frac{\pi}{40{,}000} \quad (1)$$

Observations that appeared to be outliers were examined closely to determine if their removal from the analysis was warranted. It was determined that there was no measurement or data recording error

Table 3
Summary statistics used for data analysis.

Species	Variable	Minimum	Maximum	Mean	Std Dev	Variable	Minimum	Maximum	Mean	Std Dev
Serviceberry	Kt	0.008	5.08	1.09	1.57	Height (cm)	10.00	200.00	77.79	61.83
(kg)	K1	0.004	1.44	0.34	0.45					
n = 28	K2	0.000	2.47	0.56	0.84	Crown area (m^2)	0.05	2.51	0.81	0.76
	K3	0.000	0.59	0.71	0.15					
	KL	0.002	0.39	0.09	0.11	Diameter (cm)	0.39	3.47	1.62	0.99
Manzanita	Kt	0.080	3.92	1.09	1.24	Height (cm)	19.00	190.00	77.13	39.32
(kg)	K1	0.004	0.62	0.20	0.20					
n = 32	K2	0.000	1.99	0.42	0.51	Crown area (m^2)	0.02	2.78	0.91	0.84
	K3	0.000	1.79	0.21	0.43					
	KL	0.004	0.97	0.26	0.28	Diameter (cm)	0.54	6.71	2.11	1.45
Chinkapin	Kt	0.023	4.27	0.87	1.15	Height (cm)	19.00	105.00	63.00	24.31
(kg)	K1	0.007	1.21	0.22	0.31					
n = 20	K2	0.000	1.96	0.32	0.48	Crown area (m^2)	0.05	2.83	0.87	0.81
	K3	0.000	0.56	0.09	0.18					
	KL	0.012	0.82	0.24	0.27	Diameter (cm)	0.45	3.91	1.82	1.02
Whitethorn	Kt	0.003	21.66	1.75	4.41	Height (cm)	6.00	193.00	52.08	41.38
(kg)	K1	0.001	2.76	0.49	0.76					
n = 27	K2	0.000	6.34	0.56	1.35	Crown area (m^2)	0.04	4.09	1.28	1.20
	K3	0.000	8.86	0.41	1.76					
	KL	0.002	1.88	0.18	0.38	Diameter (cm)	0.26	8.88	1.86	1.74
Deerbrush	Kt	0.012	3.65	0.48	0.84	Height (cm)	31.00	122.00	64.71	28.03
(kg)	K1	0.008	2.01	0.23	0.44					
n = 21	K2	0.000	0.93	0.15	0.24	Crown area (m^2)	0.13	4.07	1.13	0.98
	K3	0.000	0.10	0.01	0.03					
	KL	0.002	0.70	0.09	0.16	Diameter (cm)	0.49	2.60	1.20	0.61
Snowbrush	Kt	0.013	8.72	1.37	1.90	Height (cm)	13.00	194.00	64.46	38.76
(kg)	K1	0.006	2.00	0.15	0.47					
n = 26	K2	0.000	3.72	0.78	0.80	Crown area (m^2)	0.05	4.49	1.34	1.22
	K3	0.000	0.78	0.15	0.24					
	KL	0.006	1.84	0.33	0.41	Diameter (cm)	0.52	4.19	1.87	0.94
Ribes spp.	Kt	0.003	8.46	0.85	1.87	Height (cm)	12.00	159.00	51.81	34.88
(kg)	K1	0.002	2.08	0.25	0.46					
n = 26	K2	0.000	3.16	0.34	0.79	Crown area (m^2)	0.03	3.99	0.92	1.04
	K3	0.000	0.41	0.04	0.09					
	KL	0.001	2.23	0.17	0.05	Diameter (cm)	0.09	3.46	1.17	0.84

involved in obtaining metrics for these shrubs. No observations were removed.

Base model for total aboveground shrub biomass as well as biomass in different fuel classes was in the form of Eq. (2).

$$y_i = \beta_0 (ca)^{\beta_1} + \varepsilon_{ij} \tag{2}$$

where y_i is total aboveground shrub biomass or biomass in different fuel classes of the i^{th} shrub, ca is the crown area calculated using Eq. (1), β_0 and β_1 are regression parameters to be estimated from the data, and ε_{ij} is a normally distributed error term associated with the jth shrub observation on the ith species. Note that, estimate of β_1 is same for all species but we obtain species specific parameters estimates for β_0 using species as an indicator variable.

Biomass equations fitted by species i.e. species-specific equations are most common. One of the disadvantage of such an approach is the lack of enough samples in each species. Assuming the species sampled in this study represent a random sample of the population of all shrub species, it is possible to fit mixed effects model with species as random effect. Temesgen et al. (2008) described the methods for predicting the response in the future dataset when mixed effects models are used and suggested that prediction accuracy can be improved substantially when subsample of response is available. Therefore, the fixed effect model (Eq. (2)) was enhanced by adding species random effect and a nonlinear mixed effects model (NMEM) was fit. Although species was not a result of a random process in our particular data set, we assumed a random process for the mixed-effect model. The general form of a NMEM for single grouping, shrub species in this study, is defined as (after Pinheiro and Bates, 2006):

$$Y_{ij} = f(\Phi_{ij}, x_{ij}) + \varepsilon_{ij}, i = 1,\ldots m, j = 1,\ldots,n_i, \tag{3}$$

where m is the number of groups (species), n_i is the number of shrub observations on the ith species, Y_{ij} is the jth shrub observation on the ith species, f is a general, real-valued, differentiable function of a group-specific parameter vector Φ_{ij} and a covariate vector x_{ij}, and ε_{ij} is a normally distributed, within group error term. Thus, the NMEM for this study was in the following form:

$$y_{ij} = (\beta_0 + b_0)(ca)^{\beta_1} + \varepsilon_{ij} \tag{4}$$

where y_{ij} is equal to the jth shrub observation on the ith species, β_0 is a p-vector of fixed population parameters, b_{ij} is a vector of jth shrub observations on the ith species or component level random effects, and ε_{ij} is a normally distributed error term associated with the jth shrub observation on the ith species.The parameter vector varies from group to group and is defined as:

$$\Phi_{ij} = A_{ij}\beta + B_{ij} b_i, b_i \sim N(0, \psi) \tag{5}$$

where β is a r x p vector of fixed effects, and b_i is a r x q vector of random effects associated with the ith species variance covariance matrix ψ. A_{ij} and B_{ij} are design matrices of size r x 1 for the fixed and random effects. It is assumed that observations corresponding to different groups are independent and that the within group errors ε_{ij} are independently distributed as $\varepsilon_{ij} \sim N(0, \sigma^2)$ and independent of b_i (Pinheiro and Bates, 2006). A power variance function defined as $Var(\varepsilon_{ij}) \sim \sigma^2 |v_{ij}|^{2\delta}$ was specified in the model to account for the heterogeneity of error variance. Here, ε_i is the model residual, σ^2 is the residual sum of squares, $v_i = \frac{1}{ca^2}$ is the weighting variable. Starting values for the parameters of NMEM were obtained by fitting a linear mixed effects model. The heteroscedasticity in the fixed effect model was also accounted for by fitting Eq. (2) with generalized nonlinear least squares and specifying the same power variance function.Results obtained from model fitting were evaluated using root mean square prediction error (RMSPE), prediction bias, and the Bayesian information criterion (BIC):

$$\text{RMSPE} = \frac{1}{n}\sum_{i=1}^{n}\sqrt{(Y_i-\widehat{Y}_i)^2}, \tag{6}$$

where Y_i is the observed biomass for the ith shrub, $\widehat{Y}_i$ is the predicted, unweighted biomass of the ith shrub, and n is the sample size. RMSPE is a measure of difference between values predicted by a model and the values actually observed from the environment that it is being modeled from after cross validation has been performed.

In statistics, bias is referred to as the difference between an estimator's expected value and the true value of the unknown parameter of interest. In the context of this study, bias is defined as the mean difference between the measured value and the predicted value of the variable of interest as in Poudel and Temesgen (2015). Leave one out cross validation was performed in order to evaluate prediction errors (RMSPE and bias). All statistical analyses were performed in R 3.4.3 (R Core Team, 2017).

3. Results

3.1. Total aboveground shrub biomass

Several allometric models were assessed for trends in the goodness of fit measures they produced. Table 4 depicts statistical summaries obtained from fitting fixed and mixed effects nonlinear models by maximum likelihood using the nlme function in R library nlme (Pinhero et al. 2018). The standard deviation of the random effect was 0.28937 and within group residual standard deviation associated with species was 0.57432. All regression coefficients were statistically significant at the 5% level of significance (p-value < 0.05).

The goodness of fit statistic (BIC) was obtained for both fixed effect and mixed effects models used to estimate total aboveground biomass. Heteroscedasticity present within the residuals was addressed by applying a weighted variance proportional to the absolute value of the predictor (crown area) raised to a constant power. The mixed effects model with species as random effect had a BIC value of 68.82 compared to the BIC value of 73.50 obtained from the fixed effect model indicating that the mixed effects model should be preferred to the fixed effect model.

Table 4
Statistical summaries resulting from the fitting of fixed and mixed effects nonlinear models using species as random effects. Standard deviation of species random effect was 0.28937.

Species	Fixed effect model Parameter Estimate (SE)		Mixed effects model Parameter Estimate (SE)		
	β_0	β_1	β_0	β_1	b_0
AMAL	0.95827 (0.11306)	1.39443 (0.04207)	0.74705 (0.12009)	1.38709 (0.04280)	0.18270
ARPA	1.26228 (0.11010)	1.39443 (0.04207)	0.74705 (0.12009)	1.38709 (0.04280)	0.45089
CASE	0.94391 (0.13446)	1.39443 (0.04207)	0.74705 (0.12009)	1.38709 (0.04280)	0.15833
CECO	0.50206 (0.11789)	1.39443 (0.04207)	0.74705 (0.12009)	1.38709 (0.04280)	−0.21138
CEIN	0.26588 (0.12590)	1.39443 (0.04207)	0.74705 (0.12009)	1.38709 (0.04280)	−0.40579
CEVE	0.76173 (0.11352)	1.39443 (0.04207)	0.74705 (0.12009)	1.38709 (0.04280)	0.01106
RISP	0.53625 (0.11410)	1.39443 (0.04207)	0.74705 (0.12009)	1.38709 (0.04280)	−0.18581

Random effects varied by species and is shown in Fig. 2, where random effect coefficients are plotted by species. Species specific (mixed effects) and population average (fixed effect) predictions of total aboveground shrub biomass are shown in Fig. 3. It is evident that the mixed effects predictions follow the observed values more closely than the fixed effect predictions. This difference is more obvious for Deerbrush whereas the predictions are almost identical for Snowbrush. Residual analysis did not show substantial problem with the model fit. The standardized residual for one plant was relatively higher than others (Fig. 4) but the values of predictors and response were within their respective distribution (total biomass of 3.03 kg and crown area of 0.69 m^2) hence were not removed from the fitting dataset. Likelihood ratio test indicated that the additional random effect associated with parameter β_1 was not necessary ($\chi^2_{(1)} = 2.41$,p−value = 0.30).

3.2. Biomass in leaves and different fuel classes

There were only 7 shrubs with biomass in 1000 h fuel class and only 71 shrubs with biomass in 100 h fuel class (Fig. 5). Therefore, these two components were combined to form a fuel class 100 or more hour (100+ hour fuel class). Table 5 provides the parameters and their standard errors obtained from nonlinear mixed effects model for biomass in leaves and different fuel classes. All fixed effects parameters for all models were statistically significant at 0.05 level of significance. Estimate of the standard deviation of species random effect was close to zero (0.00003) for biomass in 100+ hour fuel class. Generally, variance of biomass is expected to increase with increasing diameter – the criterion used in fuel class determination. Thus, we believe that the smaller standard deviation of random coefficient in 100+ hour class could be due to the smaller sample size per species in this fuel class. Random effect coefficient was the most variable for model for 10 h fuel class (standard deviation 0.1382).

Fig. 6 depicts fitted values versus standardized residuals for different component models. These plots suggest reasonable fits for all the components with no obvious trends present in the residuals. The plots show that the NMEM is accounting for variability between species and most biomass components adequately. Higher variability in the standardized residuals for which the fitted values were less than 0.5 kg except for 100+ hour fuel class (Fig. 6). Other weighting options could be implemented, however, given the allometric relationships existing within these shrubs, a certain amount of heteroscedasticity may always be present.

3.3. Prediction error and variance

RMSPE and mean prediction bias obtained from leave-one-out cross validation are shown in Table 6. The leave-one-out cross validation RMSPE obtained from the weighted nonlinear mixed effects model for total aboveground shrub biomass was equal to 0.9249 kg (94.7 percent of mean shrub biomass) and mean prediction bias was equal to 0.0409 kg (4.2 percent of mean). RMSPE (as percent of mean) was highest for the 100 + hour fuel class whereas the bias was highest for the leaves. Interestingly, the cross-validated mean prediction bias was smallest for 100 + hour fuel class.

4. Discussion

Nonlinear mixed effects models are important tools used in growth and yield modeling. These models account the varying degrees of hierarchy within data and can provide species specific, individual predictions (Temesgen et al. 2008, Ou et al., 2016). NMEM also allow the modeler to account for several sources of heterogeneity and correlation that is present within the data (Hall and Clutter, 2004). These benefits make NMEM an attractive option for those interested in biomass estimation.

NMEM contain two standard approaches in which variation in the

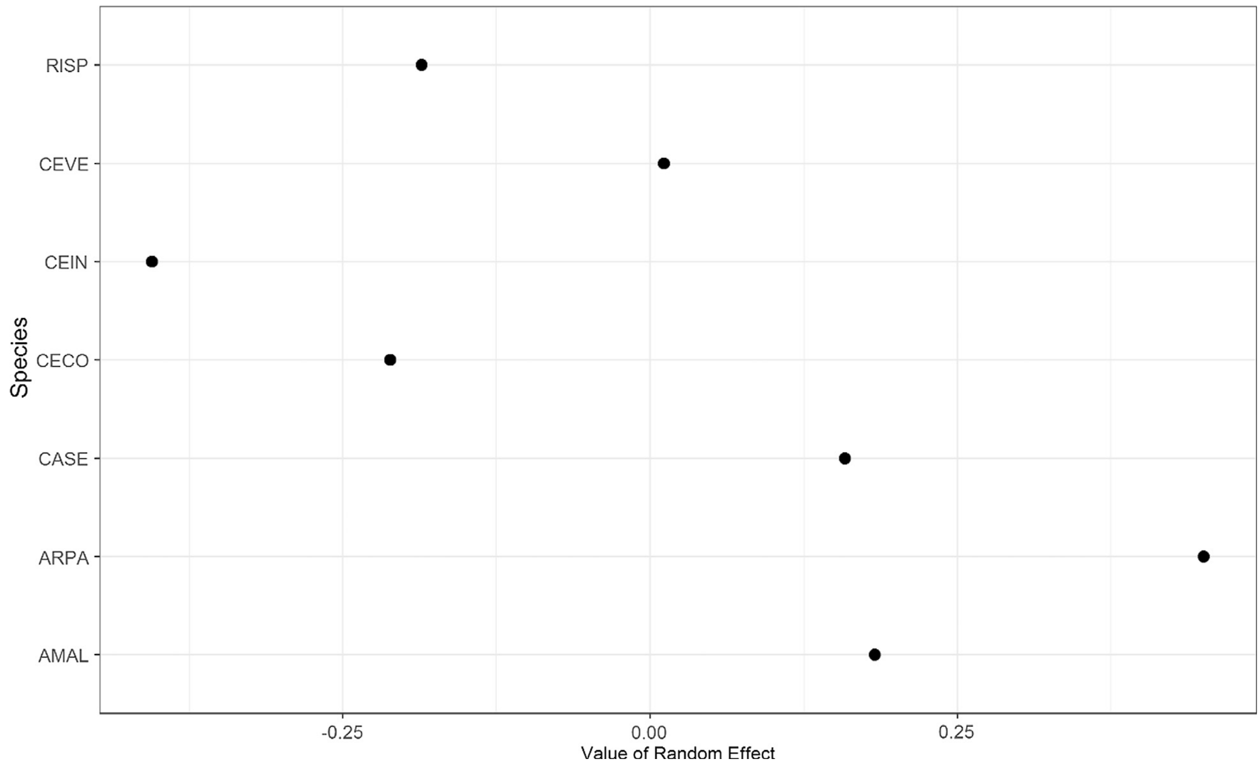

Fig. 2. Dotplot of random effect by shrub species obtained from fitting nonlinear mixed effects model. Species are AMAL = Serviceberry; ARPA = Greenleaf manzanita; CASE = Bush chinkapin; CECO = Mountain whitethorn; CEIN = Deerbrush; CEVE = Snowbrush; and RISP = Ribes spp.

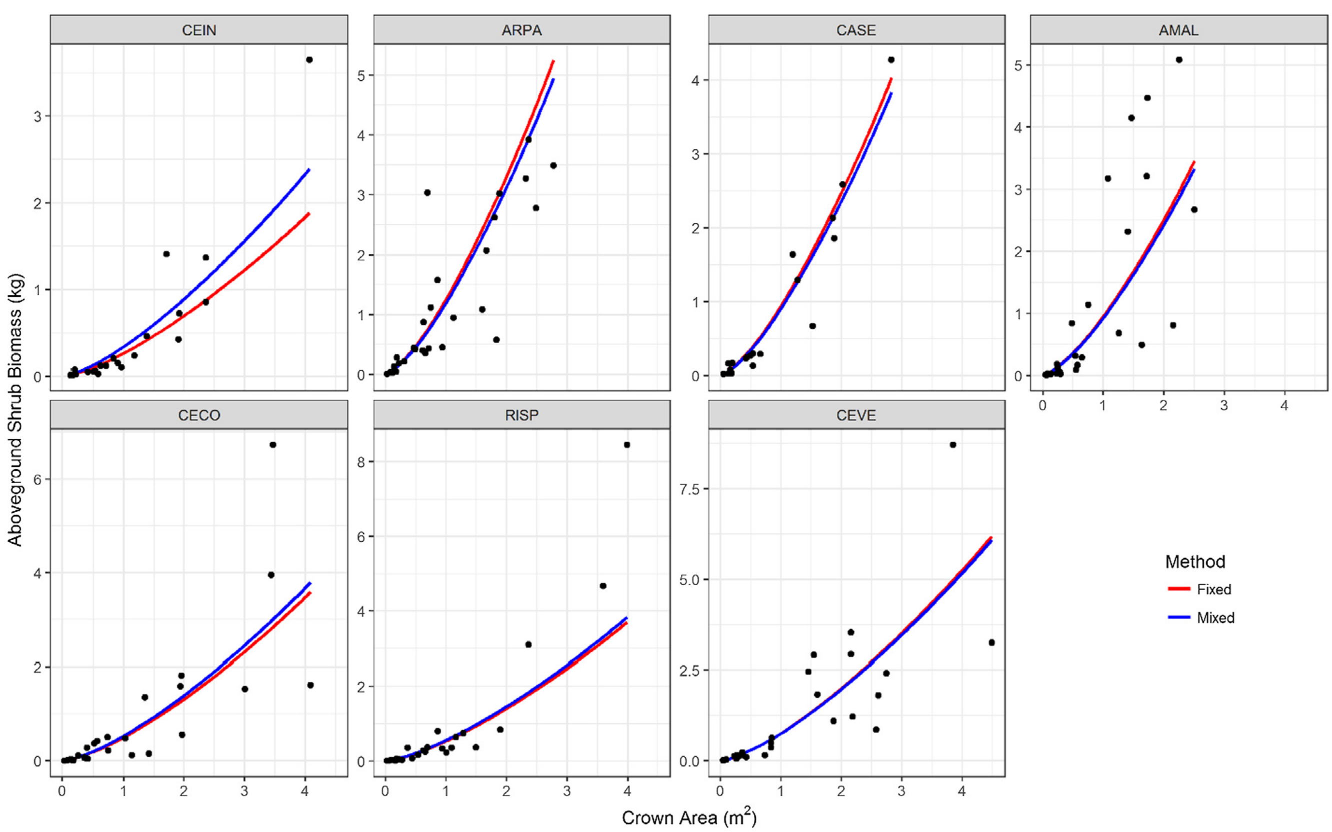

Fig. 3. Predicted total aboveground shrub biomass versus crown area for the fixed and mixed effects nonlinear regression models. Black dots are the observed values of total aboveground shrub biomass. Species are AMAL = Serviceberry; ARPA = Greenleaf manzanita; CASE = Bush chinkapin; CECO = Mountain whitethorn; CEIN = Deerbrush; CEVE = Snowbrush; and RISP = Ribes spp.

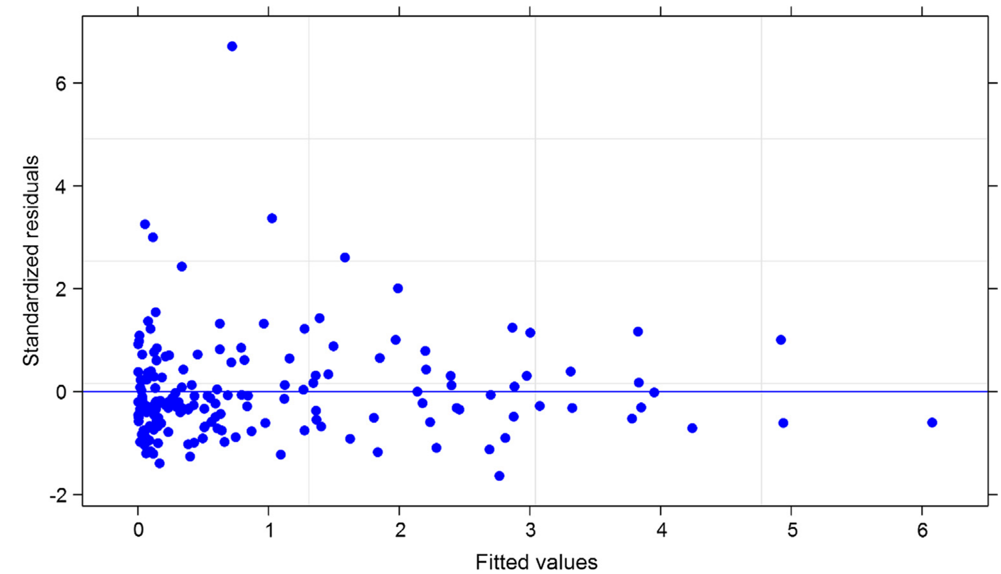

Fig. 4. Fitted values versus standardized residuals obtained by fitting nonlinear mixed effects model to predict total aboveground shrub biomass.

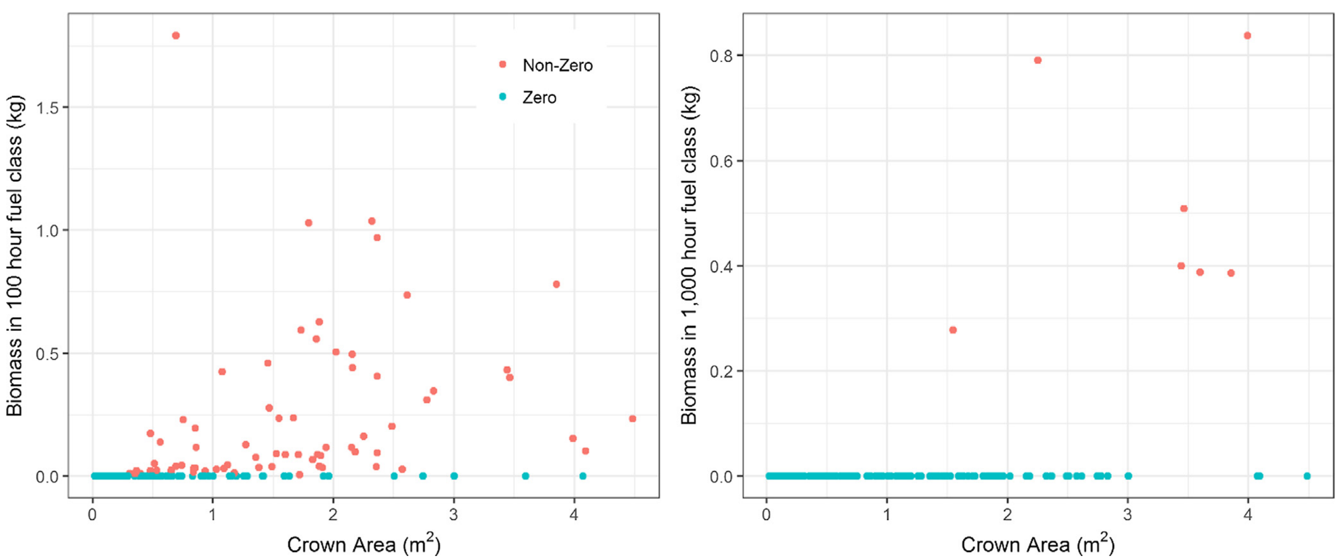

Fig. 5. Shrubs with zero and non-zero biomass in 100 and 1000 h fuel classes. There were only 7 and 71 shrubs with biomass in 1000 and 100 h fuel classes respectively.

unit effect is modeled: fixed and random effects. A drawback of fixed effects models is that they require the estimation of a parameter for each unit, which is the coefficient on the unit dummy variable (Clark and Linzer, 2012). Random effects specification models some parameters as arising from a distribution with a finite and estimable variance, which was beneficial in determining variation between shrub species. Random effects models do not involve the estimation of a set of dummy variables, but instead use the mean and standard deviation of the distribution of the unit effects (Clark and Linzer, 2012). The units in the dataset also do not have to have been drawn from a larger, normally distributed population to assume a random effects specification (Greene, 2008). A NMEM, in this setting, required fewer parameters to estimate, which leaves room for improvement in the estimation and also resulted in an efficient use of time.

There may be some confusion concerning treating species as random effects. While it is true that treating species as a random effect when there are large numbers of species is beneficial in a mixed model analysis, using species as a random effect in this setting would be useful for applications outside of the study area, the Lassen National Forest, as well as for regional application. The between-individual and within-individual variability estimated by NMEM in this study performed better than the fixed effects model.

There was some degree of variation present between random effect parameters. For example, the greatest difference between random effects could be found in the total and 10 h fuel class. There is little variation between species in the 100 + hour fuel class as indicated by the near-zero standard deviation of the random effect parameter. Fig. 3 shows that there is little to no difference in estimates from fixed and mixed effects models. In other words, a population average model is reasonable in the case of snowbrush. The largest difference in regression curves was observed in Deerbrush which is usually smaller in height compared to other shrubs, like serviceberry or Greenleaf manzanita.

There may be instances where it may be unclear as to which coefficients should be used because the random and fixed effect coefficients are similar. The modeler should examine each of the random effects for b_0 and compare them to the fixed effects coefficients and confidence intervals obtained from the model fit. Random effects should only be

Table 5
Parameter estimates and their standard errors obtained from fitting nonlinear mixed effects model for biomass in different fuel class treating species as random. φ is the standard deviation of species random effect.

Component	Species	Parameter Estimate (SE)			
		b_0	β_0	β_1	φ
Leaves	AMAL	−0.06482	0.15798 (0.03610)	1.12651 (0.03463)	0.09217
	ARPA	0.13646	0.15798 (0.03610)	1.12651 (0.03463)	0.09217
	CASE	0.11212	0.15798 (0.03610)	1.12651 (0.03463)	0.09217
	CECO	−0.07487	0.15798 (0.03610)	1.12651 (0.03463)	0.09217
	CEIN	−0.10196	0.15798 (0.03610)	1.12651 (0.03463)	0.09217
	CEVE	0.04701	0.15798 (0.03610)	1.12651 (0.03463)	0.09217
	RISP	−0.05394	0.15798 (0.03610)	1.12651 (0.03463)	0.09217
1 h	AMAL	0.09048	0.23910 (0.02396)	1.27016 (0.03829)	0.05367
	ARPA	0.01993	0.23910 (0.02396)	1.27016 (0.03829)	0.05367
	CASE	−0.00157	0.23910 (0.02396)	1.27016 (0.03829)	0.05367
	CECO	0.00615	0.23910 (0.02396)	1.27016 (0.03829)	0.05367
	CEIN	−0.07658	0.23910 (0.02396)	1.27016 (0.03829)	0.05367
	CEVE	−0.01641	0.23910 (0.02396)	1.27016 (0.03829)	0.05367
	RISP	−0.02202	0.23910 (0.02396)	1.27016 (0.03829)	0.05367
10 h	AMAL	0.22501	0.27802 (0.05595)	1.57056 (0.06585)	0.13820
	ARPA	0.13586	0.27802 (0.05595)	1.57056 (0.06585)	0.13820
	CASE	0.02334	0.27802 (0.05595)	1.57056 (0.06585)	0.13820
	CECO	−0.11433	0.27802 (0.05595)	1.57056 (0.06585)	0.13820
	CEIN	−0.17247	0.27802 (0.05595)	1.57056 (0.06585)	0.13820
	CEVE	−0.02818	0.27802 (0.05595)	1.57056 (0.06585)	0.13820
	RISP	−0.06924	0.27802 (0.05595)	1.57056 (0.06585)	0.13820
⩾100 h	AMAL	7.17E−09	0.17676 (0.04718)	0.92169 (0.27304)	0.00003
	ARPA	2.39E−08	0.17676 (0.04718)	0.92169 (0.27304)	0.00003
	CASE	−2.45E−09	0.17676 (0.04718)	0.92169 (0.27304)	0.00003
	CECO	−4.69E−09	0.17676 (0.04718)	0.92169 (0.27304)	0.00003
	CEIN	−1.66E−08	0.17676 (0.04718)	0.92169 (0.27304)	0.00003
	CEVE	−3.82E−09	0.17676 (0.04718)	0.92169 (0.27304)	0.00003
	RISP	−3.54E−09	0.17676 (0.04718)	0.92169 (0.27304)	0.00003

used if there is not a significant difference between the fixed and random effect coefficients. A significant difference indicates that bias is present within the random effect fit estimate and that the fixed effects coefficients should be used instead (Clark and Linzer, 2015). A tradeoff between fixed and random effects is that the fixed effects will provide unbiased estimates of β, but these estimates may possess large sample to sample variability. The random effects, on the other hand, will introduce bias in β estimates, but will also constrain the variance of these estimates (Clark and Linzer, 2015). The random effect model approach can lead to estimates that are closer, on average, to the true value of the sample. The random effect coefficients obtained differed by species with standard deviation of random effect coefficients ranging from −0.40579 to 0.45089 for total aboveground shrub biomass and from 0.00003 to 0.13820 for different components.

Morphological changes that ensue among species, along with intraspecific differences caused by climatic and other environmental factors, require that separate equations be used to estimate biomass in varying regions (Gregoire and Schabenberger, 1996). Shrub biomass accumulation and growth may vary from site to site and from region to region. Ou et al. (2016) found that adding topographic variables (elevation, degree of slope, and aspect) as a fixed effect to a NMEM using height and DBH as predictors improved values of AIC and BIC. Ou et al. (2016) also found that aboveground biomass of individual Simao pine (*Pinus kesiya* var. *langbianensis*) trees decreased with increasing elevation. Seeing that plant associations, such as the Jeffery pine/white fir/greenleaf manzanita/snowbrush and the California red fir/white fir/bush chinkapin communities are found at varying elevations within Lassen National Forest, obtaining measures of aspect, altitude, and degree of slope could help to better understand variability in biomass that may occur with changing topography.

Greenleaf manzanita, bush chinkapin, and deerbrush did not have any 1000-h observations. Therefore, the 100 and 1000 h fuel classes were combined to form a 100 + hour fuel class. This allowed us to fit mixed effects model for all shrub species. It should be noted that the application of mixed effects model to new species require the user to obtain a small sample those species. Additional details on how to obtain random effect parameter for new "group" (species in our case) are discussed in detail in Temesgen et al. (2008).

5. Conclusion

The use of a NMEM to quantify biomass across biomass components was beneficial in explaining the between species differences in shrub biomass common to northeastern California. The advantage of using a NMEM over a fixed effect model in this setting was evident in the reduced number of parameters that needed to be estimated using a NMEM, which saves time and allows room for improvements in the estimation. NMEM are valuable tools that are frequently employed in the field of forestry for growth and yield determination. The ability to account for multiple sources of heteroscedasticity found in data by means of random effects make NMEM an attractive option for biomass estimation. Shrub species were used as the random effects of the NMEM used to estimate total aboveground shrub biomass as well as the biomass present in different fuel classes.

The random effects used in this study did a reasonable job in accounting for larger observations of shrub biomass that were not able to be fit by the fixed effect parameters alone. Standard deviation of the random effect was the largest for total aboveground shrub biomass and the smallest for the biomass in 100 + hour fuel class. The models fitted in this study would be appropriate for modeling new shrubs that have ecological characteristics and allometric features similar to shrubs presented within this study.

Many forest management decisions are based on projections of growth and yield and the use of NMEM allows for accurate future predictions involving repeated measurements over time. NMEM were able to account for within group variation better than fixed effects

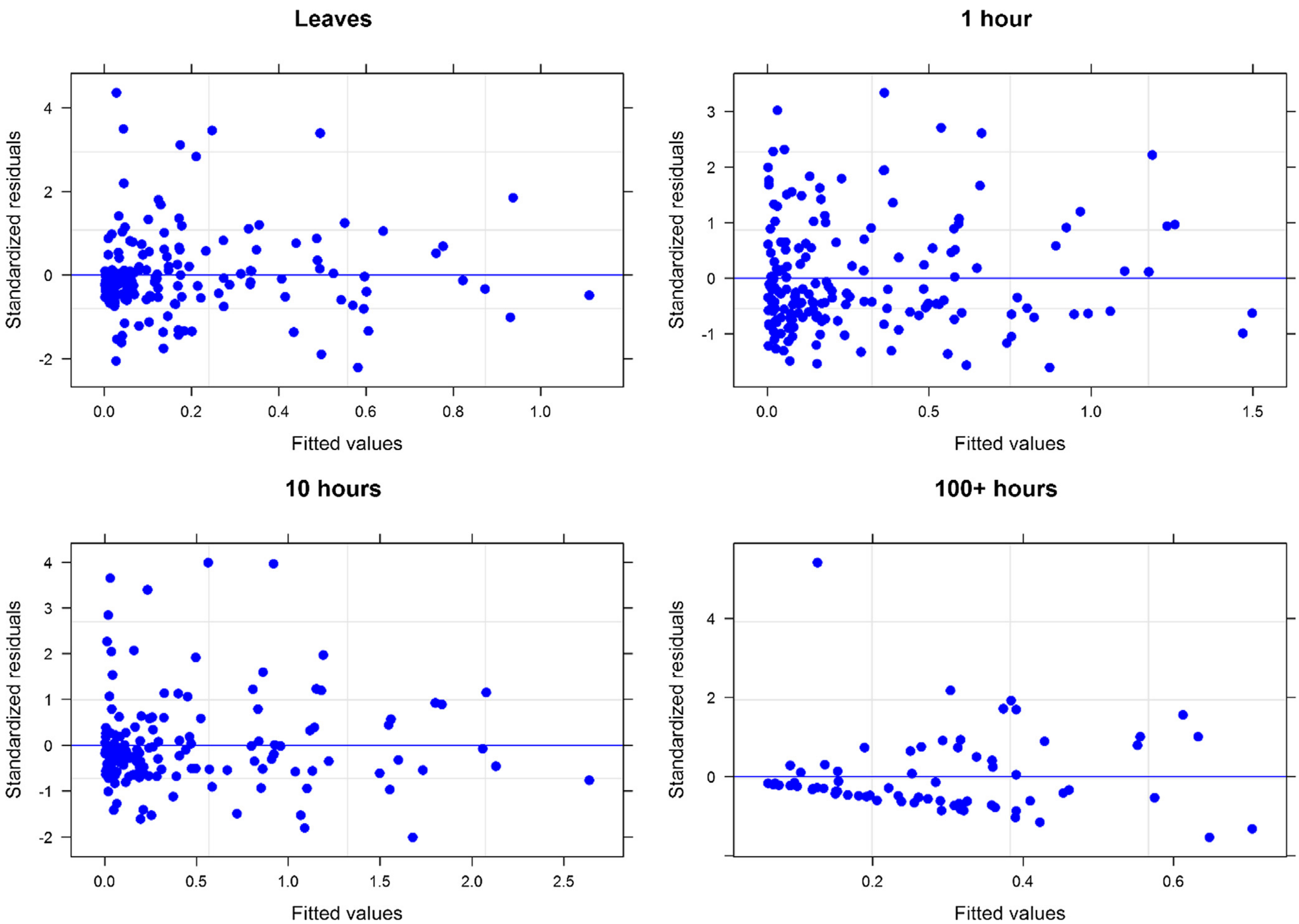

Fig. 6. Fitted values versus standardized residuals obtained by fitting nonlinear mixed effects model to predict biomass in leaves and different fuel classes.

Table 6
Bias, bias percent, RMSPE, and RMSPE percent obtained from leave one (plant) out cross validation with species as random effect.

Component	Bias	Percent Bias	RMSPE	Percent RMSPE
Leaves	0.0145	7.8	0.1930	103.8
1 h	0.0062	2.2	0.2736	95.3
10 h	0.0064	1.5	0.4280	100.2
⩾ 100 h	−0.0008	−0.3	0.3411	121.2
Total	0.0409	4.2	0.9249	94.7

parameters were able to. When fixed effect models were fitted by species, not all regression parameters were statistically significant. Additionally, the NMEM were efficient and only a single model had to be fitted. The applicability of NMEM with respect to hierarchical data makes such models attractive and practical options in forest growth and yield modeling.

This study confirms that while there is a great deal of variability present in shrub biomass, there are several methods to consider that are effective in accounting for such fluctuations. Although shrub metrics may be time consuming and somewhat arduous to obtain in the field, these woody plants must be accounted for when estimating total forest biomass. Complete estimates of total forest biomass are necessary in order to account for carbon sequestration and fuel loading in northeastern California forests. The findings resulting from this research will also help in addressing uncertainty pertaining to the efficiency of methods used to quantify component and total aboveground shrub biomass.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.04.043.

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