

Morpho-physiological traits and biomass scaling of the invasive Callery pear (*Pyrus calleryana* Decne.)

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Citation: Sharma P., Coyle D.R., Palmer J.F., Timilsina N., Hartshorn J. (2026): Morpho-physiological traits and biomass scaling of the invasive Callery pear (*Pyrus calleryana* Decne.). J. For. Sci., 72: 441–454.

Abstract: Accurately estimating aboveground biomass (AGB) of invasive plant species is essential for understanding their prevalence, ecological impacts, and informed management strategies. *Pyrus calleryana* (Callery pear) is established throughout the eastern United States, yet species-specific biomass models and physiological trait data remain limited. We destructively sampled 40 single-stem trees with diameter at breast height (DBH) ranging from 1.2 cm to 17.7 cm and height from 1.6 m to 10.3 m across six sites in South Carolina to quantify dry biomass, moisture content (MC), Carbon and Nitrogen ratios (C:N), and to develop allometric equations for predicting total AGB. The DBH-based log-linear model provided the strongest overall fit for total AGB ($R^2 = 0.91$; bias = 0.41 kg), and hold-out validation indicated strong predictive performance for unobserved trees (root mean square error, i.e. RMSE = 5.59 kg; validation $R^2 = 0.967$). Tissue traits differed significantly: leaves had the highest moisture content, whereas stems had the highest C:N ratio and AGB. These findings provide a practical, biologically interpretable DBH-based equation and biomass data suitable for forest inventory applications and invasion monitoring. The study also establishes baseline physiological parameters for *P. calleryana*, supporting improved evaluation of its ecological footprint and management needs.

Keywords: allometric modelling; Bradford pear; carbon; moisture content; South Carolina

Invasive species impose substantial economic burdens on entities of all sizes; management costs in the United States alone exceed USD 1.22 trillion since 1960, including more than USD 17 billion in the southeastern region (Fantle-Lepczyk et al. 2022). Invasive plants [i.e. non-native plants that can harm the economy, environment, and/or human health (Clinton 1999)] can negatively affect the di-

versity and community composition of native flora by competing for space and resources (Gioria, Osborne 2014; Gaertner et al. 2009). These impacts extend to nutrient cycling, ecosystem services, and regeneration potential, creating challenges for forest productivity and long-term management (Eviner et al. 2012). Given these ecological and economic pressures, improved quantification of invasive plant

presence and impact is critical for informing effective management strategies.

Accurate accounting of invasive plant biomass represents a key knowledge gap in many natural landscapes. Biomass of a species directly affects carbon storage, competitive growth and physiological dynamics, nutrient cycling, fuel loads, and other variables central to forest planning and management (Favero et al. 2020; Zhang et al. 2023). Despite its importance, the biomass of non-native woody species is often not quantified with the same priority as that of commercial or native tree species. Biomass equations describe how tree components scale with size (Gayon 2000) and are widely used for estimating biomass in hardwoods, pines, and other managed species (Tahvanainen, Forss 2008; Munsell, Fox 2010; Poudel, Temesgen 2016; Jenkins et al. 2003). Although generic and family-specific biomass equations have been used to estimate biomass (Chave et al. 2005; Chojnacky et al. 2014), species-specific biomass equations provide more accurate estimates. Species differ in their architecture and biomass allocation, especially among angiosperms, and the allometric relationship between the tree size and biomass varies among species

(Cole, Ewel 2006; Van Breugel et al. 2011). Equations developed for a group of species or genera may be useful for global or regional predictions, but they are not well-suited to localised biomass predictions for a particular species biomass (Cole, Ewel 2006; Van Breugel 2011). Limited availability of species-specific biomass models for invasive trees constrains the ability of land managers to evaluate ecological impacts, assess carbon consequences, or estimate management costs and effort (Khanna, Chaturvedi 1982; Burkhart, Tomé 2012).

Callery pear (*Pyrus calleryana* Decne.) (Figure 1) is an increasingly problematic invasive tree in the eastern United States.

Originally introduced as a rootstock and ornamental species (Culley et al. 2011), Callery pear now occurs in at least 37 states and is considered invasive in 13 of those (Center for Invasive Species and Ecosystem Health 2025). Its rapid spread is facilitated by abundant fruit production (Culley 2011), bird-mediated seed dispersal (Clark 2022), tolerance of disturbed sites (Dunn 2018; Hay 2021), high pollinator visitation that enhances cross-pollination (Sharma et al. 2025), and vigorous resprouting following cutting or burning (Maloney 2021;

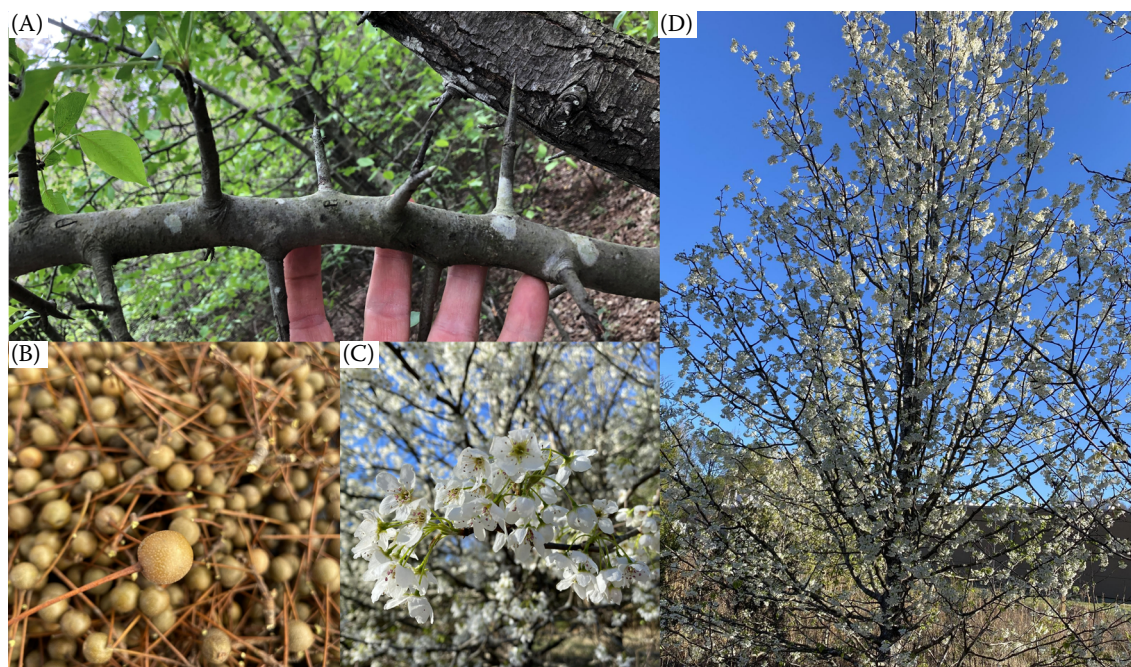


Figure 1. Callery pear branches are often loaded with thorns (A) which can injure livestock and damage equipment; fruits (B) have a range in size from peas to ping-pong balls, and each fruit contains several seeds; flowers (C) are most known from the flowering Bradford pear tree, the domesticated cultivar of the Callery pear tree; Callery pear trees in full bloom (D) are often the first flowers seen on woody species throughout its range

Photo: A – David R. Coyle; B–D – Prabina Sharma

<https://doi.org/10.17221/49/2026-JFS>

Woods et al. 2021). Additional management challenges include large thorns (Vincent 2005; Coyle et al. 2021) and release from natural enemies (Hartshorn et al. 2022), which enable seedlings and saplings to escape browsing pressure and form dense stands that displace native vegetation. As Callery pear invasions expand, understanding aboveground biomass and tissue characteristics becomes essential for estimating the ecological footprint and management burden of Callery pear.

Callery pear can be detected on the landscape using digital imagery (Awasthi et al. 2025), but this technology currently lacks the ability to determine fine-scale details about its prevalence and potential impact. Aboveground biomass models can provide this information and support forest managers by providing reliable estimates of total biomass, carbon storage, and management needs, as well as insight into species-specific resource allocation patterns (Boyce, Ocasio 2020; Pattison et al. 1998). Despite growing concern regarding the ecological impacts of Callery pear, information pertaining to its *MC* and *C:N* is unknown, and allometric equations specific to this species have not been developed. These gaps limit the ability of forest managers to accurately assess and plan for the impacts of Callery pear in invaded systems. To address these knowledge gaps, our objectives were to: (i) quantify aboveground biomass (*AGB*) and other physiological and morphological characteristics of Callery pear, and (ii) develop and validate allometric equations for predicting Callery pear biomass.

MATERIAL AND METHODS

Site description. We selected six study sites in Western and Central South Carolina, United States (Table 1) based on confirmed Callery pear presence, permission for destructive sampling,

accessibility for field processing, availability of single-stem individuals across a range of diameter at breast height (*DBH*) classes, and separation among sites to reduce spatial dependence. These sites were chosen specifically to be representative of Callery pear invasion in the eastern United States, that is, a monoculture of dense Callery pear across a range of diameters and size classes. All the sites consisted of predominantly well-drained Ultisols. The statewide annual average temperature is approximately 16.7 °C (62 °F), and average annual precipitation is 121.4 cm (47.8 in.) (South Carolina State Climatology Office 2020). The sampled areas were visually dominated by Callery pear with some other woody species observed within the broader set of study sites, including various pine species (primarily *Pinus taeda* L. and *Pinus virginiana* Mill.), oak species (primarily *Quercus nigra* L. and *Q. falcata* Michx.), black cherry (*Prunus serotina* Ehrh.), and sweetgum (*Liquidambar styraciflua* L.). Thorny vines (e.g. *Smilax rotundifolia* L.) and various forbs and grasses were also present.

Destructive sampling. We felled single-stem Callery pear trees across a range of size classes in August and September of 2021 ($n = 8$) and 2022 ($n = 32$). Single-stem trees were defined as individuals without forking below breast height (1.37 m); trees forking at or below breast height were excluded to ensure consistent *DBH* measurement. Prior to felling, we recorded the diameter at breast height (*DBH*) of each stem. We then cut each tree as close to the ground as possible (< 5 cm), measured total tree height and separated aboveground tissue components into leaf, branch, and stem immediately on a tarp on the ground in the field.

For small trees ($DBH < 7$ cm), we destructively sampled all aboveground tissues, placed components in labelled paper bags, transported them to the Clemson University Forest Health Labora-

Table 1. Study sites in South Carolina were at least 2 km apart and considered independent of each other

Site name	Latitude	Longitude	Elevation (m a.s.l.)	County	Number of trees sampled
Ingles	34°42'13"N	82°47'39"W	305	Pickens	8
Water Plant	34°38'19"N	82°46'25"W	290	Anderson	7
Campground	34°37'32"N	82°46'47"W	295	Anderson	7
Piedmont	34°44'45"N	82°28'16"W	265	Anderson	7
Greenville	34°49'24"N	82°28'11"W	250	Greenville	6
Sandhill	4°08'19"N	0°52'15"W	85	Richland	5

tory, and recorded green mass for each component prior to drying. Trees with $DBH < 7$ cm were processed in full because all aboveground tissues could be transported, dried, and weighed directly. Trees with $DBH \geq 7$ cm produced substantially larger biomass volumes; therefore, representative tissue subsamples were used to estimate whole-tree dry mass. This threshold was operational rather than biological and was selected to maintain consistent and feasible processing across the sampled size range. For larger trees ($DBH > 7$ cm), we first measured whole-tree green mass (kg) in the field using a hanging scale (HME Digital, United States) after felling and bundling the tree in a tarp. Because entire trees could not be accommodated in the drying ovens, we subsampled tissues to represent approximately 10% of the total green mass of each tissue component (i.e. foliage, branches, and stem) using visual estimation in the field. Only these subsamples were transported to the laboratory, where the subsample wet biomass was recorded using a bench scale (RC6RS, United States) for foliage and branches and a platform scale (Fisher Scientific, United States) for larger stem subsamples. All subsamples of larger trees and whole smaller trees were dried in a convection oven (Lindberg 146 series, United States) at 100 °C for 48–72 h to constant mass (Khanna, Chaturvedi 1982) and re-weighed using the same scales.

We then divided the whole tree into three equal sections: main stem below the start of the canopy, mid-canopy at the crown onset, and the upper/apical meristem. For large trees, component-specific dry-to-wet biomass ratios derived from subsamples were extrapolated to whole-tree measurements by scaling each component separately to the measured whole-tree green mass (i.e. subsample wet biomasses were used to estimate component wet biomass proportions and corresponding conversion to oven-dry biomass), and component dry biomasses were summed to obtain total oven-dry *AGB* per tree.

Moisture content (*MC*) was quantified consistently for both small and large trees. For stem, we divided it into three equal-length sections (lower bole below crown onset, mid-bole at crown onset, and upper bole) and cut a 2.54 cm (1 in.) thick cookie (i.e. cross-cut section) from the base of each section. Cookies were weighed fresh, oven-dried alongside other samples, and re-weighed for *MC* analysis. To calculate *MC* (%), we used Equation (1):

$$MC(\%) = \frac{W - D}{W} \times 100 \quad (1)$$

where:

W – wet weight;

D – dry weight.

After all samples were dried and weighed, we took a subsample of each tissue component from each of the 40 trees and ground them separately into a fine powder using a Wiley electric mill (Thomas Scientific, United States) with a 2 mm mesh. Each ground sample was individually packaged in a labelled paper bag and sent to the Clemson Agricultural Services Laboratory to quantify C and N. The amount of C was then divided by the amount of N to determine each component's C:N ratio for each tree.

Statistical analysis. To evaluate the relationship between biomass of individual tissue components and *DBH*, we fitted linear regression models for tissue-specific biomass vs *DBH*. Total C:N was modelled as a function of *DBH* using ordinary least squares. Differences among tissue types (stem, branch, leaf) were analysed using a repeated-measures ANOVA with tissue as a fixed effect and tree included as the subject factor. Post hoc pairwise comparisons were conducted using Tukey's adjustment. To evaluate the contribution of tree height, we assessed the relationship between *DBH* and height using Pearson's correlation. Because *DBH* and height were strongly positively correlated, height was excluded from the final models to avoid multicollinearity and maintain model parsimony.

Allometric equations and validation. We developed and evaluated biomass allometric models based on a systematic literature review and exploratory data visualisation (Jenkins et al. 2003; Jiang et al. 2013; Timilsina et al. 2014). Two commonly used model forms were evaluated for total dry biomass models: (i) a log–log linear model fitted on the transformed scale, and (ii) a quadratic model fitted on the original biomass scale. Because the objective was to develop an operational *DBH*-based biomass equation that can be applied to new trees without requiring site-specific calibration data, candidate equations were compared and validated as fixed-effect models using ordinary least squares (OLS).

The biomass–diameter relationship in trees is well established as an allometric (power-law) pattern, typically expressed as Equation (2) (Chojnacky et al. 2014):

<https://doi.org/10.17221/49/2026-JFS>

$$W = a \times DBH^b \quad (2)$$

where:

- a – scaling coefficient (intercept of the allometric equation);
- b – allometric exponent (slope parameter);
- DBH – diameter at breast height.

To facilitate parameter estimation and meet statistical assumptions, we applied a log transformation, resulting in the log-linear form shown as Equation (3):

$$\ln(D) = \beta_0 + \beta_{DBH} \ln(DBH) \quad (3)$$

where:

- β_0 – intercept on the log-transformed scale.

Log-transformed regression has been consistently used to fit these models (e.g. Jenkins et al. 2003; Chojnacki et al. 2014; Clough et al. 2016). Parameters for the log-transformed model (Model 1) were estimated and back-transformed to the original scale using Duan's smearing estimator (Duan 1983) to reduce retransformation bias. A quadratic model fitted on the original scale (Model 2) was also evaluated for comparison. Equations (4) and (5) show the model formulations:

$$\text{Model 1: } \ln(W) = \beta_0 + \beta_1 \ln(DBH) \quad (4)$$

$$\text{Model 2: } W = \beta_0 + \beta_1 DBH + \beta_2 DBH^2 \quad (5)$$

where:

- W – response variable;
- DBH – predictive variable;
- β_0, β_1 – allometric constants.

Model performance was evaluated using bias, root mean square error ($RMSE$), R^2 , Akaike information criterion ($AICc$), and Bayesian information criterion (BIC). Because trees were sampled within six sites, we also fitted a site random-intercept version of the selected log–log model as a sensitivity analysis to evaluate whether residual site-level variation remained after accounting for DBH . This mixed-effects analysis was used to assess site-level heterogeneity, whereas the final predictive equation and hold-out validation were based on the fixed-effect DBH -only equation. As part of model evaluation, we also examined whether inclusion of additional predictors

improved model performance, an extended log–log formulation incorporating tree height was tested, i.e. $[\log(W) = \beta_0 + \beta_1 \log(DBH) + \beta_2 \log(HT)]$.

Results show that total dry biomass was significantly related to DBH ($t = 6.75$; $P < 0.0001$) but adding height did not improve model performance ($t = -0.30$, $P = 0.768$); therefore, DBH -only models were retained for subsequent analyses. This approach aligns with common forestry practice, in which DBH explains most of the biomass variation and is measured consistently across spatial scales (Burkhart, Tomé 2012; Jenkins et al. 2014). Site (location) was included as a random effect to account for the hierarchical structure of the data and to support inference beyond the specific sampling locations.

All analyses were conducted in Python 3.10 (Van Rossum, Drake 2009), using pandas 1.5 (McKinney 2010) for data handling, Statsmodels 0.14 (Seabold, Perktold 2010) for linear modelling, SciPy 1.11 (Virtanen et al. 2020) for nonlinear fitting, and Matplotlib 3.7 (Hunter 2007) for visualisation. Because biomass to size relationships are typically multiplicative, log-log models were back-transformed using Duan's smearing estimator to remove bias in predictions on the original scale and model performance was evaluated on the original biomass scale using bias and $RMSE$ (%) on the original W scale, see Equations (6) and (7):

$$Bias = \frac{1}{n} \sum_{i=1}^n (\hat{W}_i - W_i) \quad (6)$$

$$RMSE\% = 100 \times \frac{\sqrt{\frac{1}{n} \sum_{i=1}^n (\hat{W}_i - W_i)^2}}{\bar{W}} \quad (7)$$

where:

- n – sample size;
- W_i – observed dry biomass;
- $\hat{W}$ – back-transformed prediction from the log model (i.e. no smearing/bias correction applied);
- $\bar{W}$ – mean observed biomass.

To compare stem, branch, and leaf tissue components, we evaluated model performance on the original mass scale (kg) using observed–predicted plots against the 1:1 line (Figure 2) and summary statistics for all the tissue components and chose the best model out of two, fitted separately for each tissue component. We reported $\hat{b}_0 = \exp(\hat{\beta}_0)$, $\hat{b}_1 = \hat{\beta}_1$, the two-sided P -value for

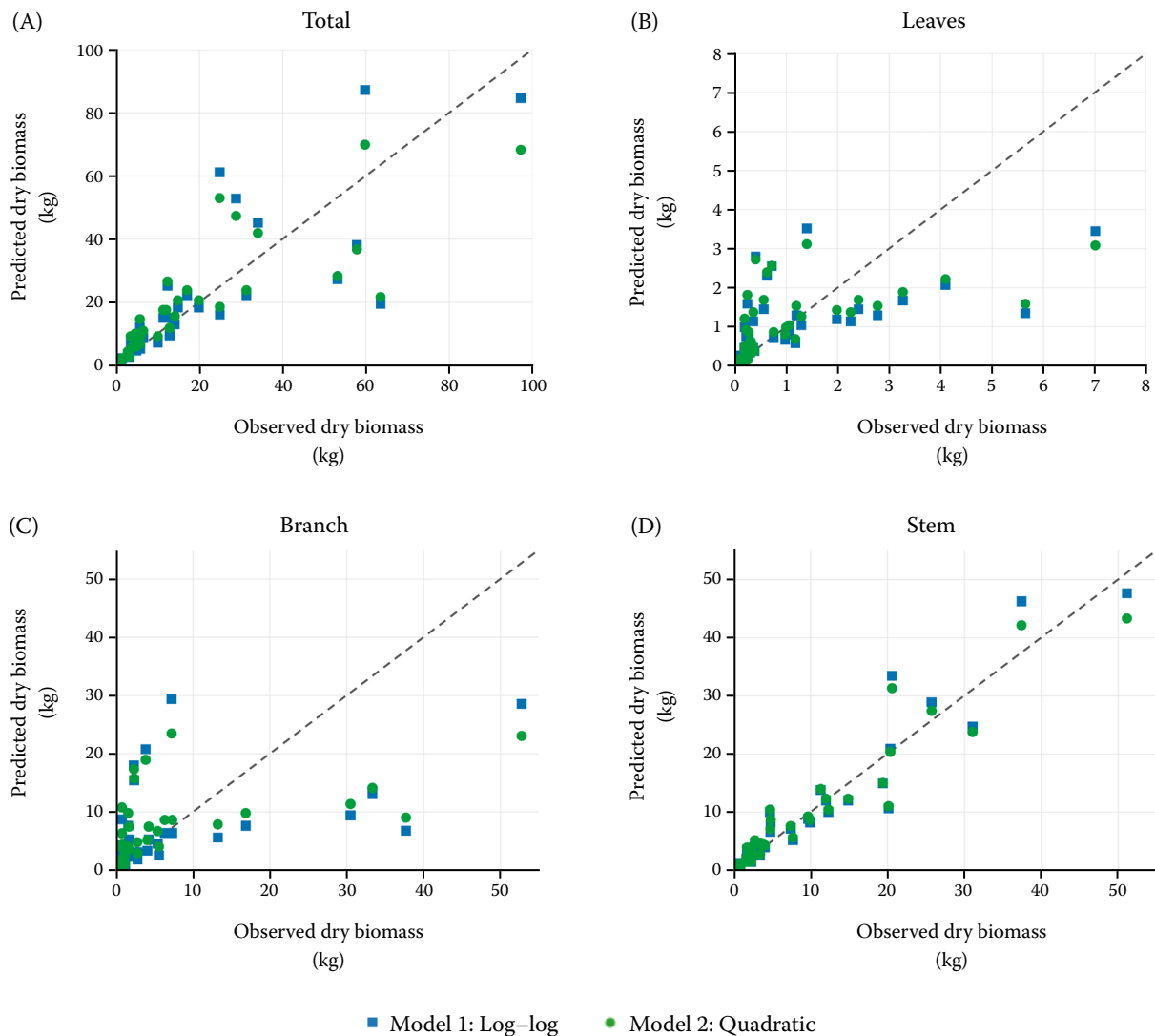


Figure 2. Observed vs predicted dry biomass (kg) for all models across tissues: A – total biomass, B – leaves, C – branches, D – stem biomass

Blue squares – Model 1; green circles – Model 2; dashed line – 1:1 agreement

the slope, and $RMSE\%$ ($RMSE$ divided by the mean observed component mass), alongside R^2 for the final model only. Since the sample size was small ($n = 40$), we used information criteria based on the small-sample corrected Akaike information criterion ($AICc$) rather than AIC and BIC .

To evaluate the robustness and generalisation of the selected biomass model, we implemented an independent hold-out validation strategy. Model selection was performed using the full dataset based on information criteria and goodness-of-fit metrics, and validation was applied only to the final selected log–log DBH model. The dataset was randomly partitioned into a training set ($n = 30$

trees) and a testing set ($n = 10$ trees), with care taken to ensure that the range of DBH values, including larger trees, was represented in both subsets. The model was fitted on the training data using ordinary least squares (OLS) on the log scale, and predictions for the test set were back-transformed to kilograms using Duan's smearing estimator (Duan 1983). This approach is widely recommended for log-transformed allometric models because naive back-transformation systematically underestimates true biomass values (Sprugel 1983). Model performance on the validation set was evaluated using R^2 , $RMSE$, and mean absolute error (MAE), see Equation (8):

<https://doi.org/10.17221/49/2026-JFS>

$$MAE = \frac{1}{n} \sum_{i=1}^n |y_i - \hat{y}_i| \quad (8)$$

where:

$y_i, \hat{y}_i$ – observed and predicted biomass (kg), respectively.

RESULTS

Morphometric characteristics. *DBH* of sampled trees ranged between 1.2–7.7 cm, and height ranged between 1.6–0.3 m. Most trees had a *DBH* of 10 cm or less (Table 2). Stem accounted for the most biomass of any sized tree, followed by branches and leaves (Table 2). Smaller trees had a higher proportion of leaf biomass, while the proportion of branch biomass varied among *DBH* classes (Table 2).

Across tissue components, wet and dry biomass was highest in the stem, followed by branches and leaves (Table 3). Total tree-level averages ($\pm$ SE) were 28.62 ± 5.78 kg for wet biomass and 16.68 ± 3.44 kg for dry biomass (Table 3).

Because tissue components were measured from the same trees, differences among tissue components were evaluated with a repeated-measures ANOVA with tree as the subject factor. This analysis revealed significant differences among tissue types [$F_{2,78} = 11.82$; $P < 0.0001$]. Post hoc pairwise comparisons using Tukey's adjustment indicated that stem biomass was significantly greater than both branch and leaf biomass, and branch biomass was greater than leaf biomass. To examine scaling relationships, tissue-specific relationships between dry biomass and *DBH* were evaluated for stems, branches, and leaves. Dry biomass increased significantly with

DBH (stem: $t = 15.33$, $P < 0.0001$; branch: $t = 4.10$, $P < 0.001$; leaves: $t = 4.16$, $P < 0.001$).

C:N ratios differed significantly among tissues [repeated-measures ANOVA: $F_{2,78} = 332.06$; $P < 0.0001$]. Stems had the highest C:N ratio (167.79 ± 6.24), followed by branches (117.69 ± 4.57), while leaves had the lowest C:N ratio (33.84 ± 0.56 ; Table 3). Post hoc pairwise comparisons confirmed the ordering stems > branches > leaves (all adjusted $P < 0.0001$).

MC differed among tissue types (repeated measures ANOVA, $F_{2,78} = 3.89$, $P = 0.0246$; Table 3), with leaves exhibiting the highest *MC*, followed by stems and branches. Holm-adjusted paired comparisons indicated that stem *MC* was higher than branch *MC* (mean difference = 2.61%; $P = 0.0044$), whereas leaf and stem *MC* did not differ ($P = 0.695$), and leaf and branch difference was also not significant ($P = 0.0716$). Across the sampled size range, *DBH* was not associated with *MC* for leaves ($P = 0.225$) or branches ($P = 0.790$), but stem *MC* declined with increasing *DBH* (-0.50% points per cm; $P = 0.007$).

Allometric equations and validation. Among the two allometric equations tested for total dry biomass, Model 1 (log-linear) provided the best fit in terms of *AICc*, *BIC* and R^2 compared to Model 2 (Table 4; Figure 2). When tree height was included in the log-linear mixed-effect model, overall performance declined, with R^2 decreasing from 0.651 (*DBH*-only) to 0.611 and *RMSE* increasing by approximately 707 units. Although the height coefficient was positive ($\beta_2 \sim 0.465$), its inclusion did not improve overall model fit. *DBH* and height were strongly positively correlated (Pearson's $r = 0.68$, $P < 0.0001$), supporting the exclusion of height from the final models.

Table 2. Allocation of biomass of Callery pear sampled in South Carolina, United States, across *DBH* classes [values represent mean proportions of total tree biomass in each tissue type for four *DBH* classes; total wet and dry biomass and number of trees (*N*) are shown for each diameter class]

<i>DBH</i> class	Wet proportion			Dry proportion			Total (kg)		<i>N</i>
	stem	branch	leaf	stem	branch	leaf	total wet	total dry	
1–5	0.58	0.27	0.12	0.59	0.28	0.11	64.84	36.36	15
5–10	0.49	0.39	0.09	0.50	0.41	0.08	476.66	275.16	18
10–15	0.57	0.32	0.04	0.58	0.36	0.04	328.50	198.82	5
15–20	0.53	0.36	0.04	0.56	0.38	0.05	274.74	156.98	2

DBH class – based on diameter at breast height (1.37 m); wet biomass – green mass prior to drying; dry biomass – oven-dry mass; tissue proportions were calculated within each *DBH* class as the sum of component biomass divided by the sum of total aboveground biomass (*AGB*) for that class (computed separately for wet and dry mass); total wet biomass (kg) and total dry biomass (kg) – the summed above ground totals for all trees within each *DBH* class; *N* – number of trees

<https://doi.org/10.17221/49/2026-JFS>Table 3. Wet and dry biomass, moisture content (*MC*), and the C:N ratio of Callery pear sampled in South Carolina, United States

Tissue component	Wet biomass (kg) ($\mu \pm \text{SE}$)	Dry biomass (kg) ($\mu \pm \text{SE}$)	<i>MC</i> (% $\pm \text{SE}$)	C:N ($\mu \pm \text{SE}$)
Stem	15.26 $\pm$ 2.98	9.15 $\pm$ 1.80	41.98 $\pm$ 0.80*	167.79 $\pm$ 6.24
Branch	10.34 $\pm$ 2.98	6.40 $\pm$ 1.86	39.37 $\pm$ 0.92*	117.69 $\pm$ 4.57
Leaf	1.95 $\pm$ 0.41	1.13 $\pm$ 0.24	42.49 $\pm$ 1.11	33.84 $\pm$ 0.56
Total	27.76 $\pm$ 5.58	16.68 $\pm$ 3.43	41.28 $\pm$ 0.65	106.44 $\pm$ 3.29

*significant stem–branch difference in *MC* at $\alpha = 0.05$; *MC* differed among tissues (one-way repeated-measures ANOVA: $F_{2,78} = 3.89$; $P = 0.0246$); within-tree paired comparisons were Holm-adjusted: stem vs branch $P = 0.0044$, stem vs leaf $P = 0.695$, and branch vs leaf $P = 0.0716$

Mixed-effects models indicated that site-level variability contributed to biomass differences beyond individual tree characteristics. The random effect of site accounted for approximately 11% of the total variance in biomass, suggesting consistent differences among locations independent of *DBH*.

The estimated elasticity of the log–linear model (Model 1) was strongly positive ($\beta_1 \sim 2.10$) with dramatically lower *AICc* and *BIC* values relative to the alternative model, indicating a superior fit when accounting for model complexity. Hence, because of the above-explained reasons, we have used the log-linear model for subsequent comparisons of tissue component models and hold-out validation. Model performance varied among tissue components, with branches and leaves exhibiting a lower R^2 value and higher *RMSE* compared to the stem, which is reasonable in the case of the Call-

ery pear tree, as their biomass varies greatly from tree to tree compared to the stem (Table 5). Table 5 summarises parameter estimates (β_0 , β_1) for all tissue components and lists the associated *RMSE* value, R^2 , and *P*-values.

When the final log–log *DBH* model was fitted to the training dataset and evaluated on the withheld testing dataset, the total biomass model achieved a root mean square error (*RMSE*) of approximately 5.59 kg, a mean absolute error (*MAE*) of 3.58 kg, and a validation R^2 of 0.967. These validation statistics describe the predictive performance of the fixed-effect operational equation for withheld trees, rather than site-specific conditional predictions from the sensitivity mixed-effects model. The *DBH* elasticity on the log scale (~ 2.10) remains highly significant ($P < 0.001$), consistent with earlier fits on the full dataset.

Table 4. Test statistics of three models tested for total biomass

Model	β_0	β_1	β_2	<i>RMSE</i> (%)	R^2	Bias (kg)	<i>AICc</i>	<i>BIC</i>
Model 1: log-log	5.3023	2.0775	–	0.074	0.913	0.41	–65.42	–62.36
Model 2: quadratic	5 290.86	2 066.26	121.55	0.071	0.695	0.00	757.09	761.49

β_0 , β_1 , β_2 – coefficients; *RMSE* – root mean square error; model's performances are assessed on the lowest *RMSE*, R^2 values and information criteria (*AICc*, *BIC*); the coefficients for Model 1 ($\alpha = e^{\beta_0}$) are not back transformed

Table 5. Individual tissue components with coefficients and goodness-of-fit parameters

Tissue	β_0	β_1	<i>RMSE</i> (%)	R^2	<i>P</i> -value (slope)
Stem	4.749	2.074	37.59	0.943	< 0.0001
Branch	4.011	2.034	159.82	0.670	< 0.0001
Leaves	4.026	1.331	117.70	0.536	< 0.0001

β_0 , β_1 – model coefficients listed for individual tissue components along with R^2 , *RMSE*, and *P*-value; *RMSE* – root mean square error

<https://doi.org/10.17221/49/2026-JFS>

DISCUSSION

Accurately quantifying *AGB* of target species is foundational to ecological modelling, C accounting, and forest management. Although generalised biomass equations exist for many North American tree species (e.g. Jenkins et al. 2003; Chojnacky et al. 2014), invasive species such as Callery pear remain underrepresented in available allometric databases. This gap limits the ability of land managers to evaluate biomass accumulation, estimate management effort, or understand Carbon consequences associated with expanding species invasions. Our work showed that the log–log (log-linear) *DBH*-only model provided the strongest performance to predict total *AGB* of the invasive Callery pear tree, yielding high explanatory power, minimal prediction bias, and clear biological interpretability. The log–log model also yielded the lowest *AICc* and *BIC* values, indicating a superior trade-off between fit and parsimony, and demonstrated the strongest explanatory power on the log scale. Loglinear allometry is widely supported in forestry because tree mass scales multiplicatively with diameter in accordance with biomechanical and hydraulic constraints, and log transformation stabilises variance and linearises this relationship (Packard 2014; Zianis, Mencuccini 2004; Mascaro et al. 2011). Moreover, applying Duan's smearing correction ensured unbiased back-transformation of predicted biomass, addressing a well-known source of bias in log-transformed allometric models (Duan 1983; Sprugel 1983). Hence, we finalised the log-linear model using only *DBH*, which aligns best with national-scale *DBH*-based models, while avoiding the added measurement burden and reduced transferability often associated with height-inclusive equations (Jenkins et al. 2003; Temesgen et al. 2015).

There is a paucity of information on Callery pear allometry and abundance despite its prevalence as an invasive species throughout the eastern United States. Previous work (Boyce, Ocasio 2020) developed allometric equations using diameter at stump height (25 cm) rather than *DBH* because Callery pear often forks below breast height; they paired this with surveys of 23 invaded stands to quantify stand structure and biomass components. Our study emphasised a *DBH*-based equation to align with inventory systems that use *DBH* as the standard predictor – including national-

scale approaches (Jenkins et al. 2003; Woodall et al. 2011; Chojnacky et al. 2014) – a choice supported by longstanding evidence that *DBH* alone is a strong, reliable indicator of tree size and *AGB* (Pastor et al. 1984; Chojnacky et al. 2014). In addition, our sampling incorporated multiple independent sites in South Carolina and explicitly quantified tissue traits (*MC* and *C:N*) not previously reported for Callery pear, thereby expanding the applicability of Callery pear biomass estimation beyond stand biomass to include trait-informed interpretations relevant to invasion effects and biomass utilisation contexts.

Non-destructive methods such as allometric equations are widely used to estimate tree biomass, though the accuracy of the equation depends on the variable used (Chave et al. 2014). Our model explained 91% of the variation in total *AGB*, and the positive bias value of 0.41 kg shows that our model overpredicts biomass by approximately 0.41 kg – this is negligible in the context of forest management as it amounts to less than a quarter of the biomass of a typical small branch. For example, branches account for about 17% of total *AGB* in both hardwood and softwood species (Jenkins et al. 2003), meaning a typical branch on a small tree can weigh roughly 0.3–0.5 kg. Moreover, the validation confirms that the *DBH*-only model performs reliably on data not used in model training, supporting its use for scientific reporting and best choice for biomass prediction. The site random-intercept model was used as a sensitivity analysis to evaluate residual site-level heterogeneity, but validation metrics should be interpreted as the predictive performance of the operational fixed-effect *DBH*-only equation rather than as site-specific conditional predictions from a mixed-effects model. For even greater rigour, repeated random splits or k-fold cross-validation could be employed to quantify variability in predictive performance (Hastie et al. 2009), but the current results already demonstrate strong generalisation and biological interpretability. Hence, the equation we developed can be added to the database which contains numerous biomass equations developed and used for many tree species in the United States (Jenkins et al. 2003; Woodall et al. 2011; Radtke et al. 2015).

Partitioning biomass revealed tissue-specific patterns in that branch and leaf components exhibited greater variability than stems, which is a well-documented feature of crown architecture and site-level

heterogeneity (Kunz et al. 2019; Hilmers et al. 2025). The dominance of stem biomass and its tight scaling with *DBH* further reinforces the utility of diameter-only models for Callery pear. Stems displayed the strongest predictive relationship, whereas branch and leaf biomass showed higher variability, a common feature of crown components influenced by site conditions, resource availability, and architectural plasticity (Coyle, Coleman 2005; Tahvanainen, Forss 2008; Coyle et al. 2016; Kunz et al. 2019). The log–log model's simplicity, interpretability (β_1 as the elasticity of biomass with respect to *DBH*), and statistical performance make it suitable for large-scale inventories where *DBH* is readily measured (Chave et al. 2004, 2014). Hold-out validation confirmed that the *DBH*-only fixed-effect equation performed well for withheld trees. The separate site random-intercept sensitivity analysis indicated some residual site-level variability, so the equation should be interpreted as a population-level biomass model applicable to similar single-stem Callery pear trees within the sampled *DBH* range.

Other variables, such as site, tree age, stem taper, and environmental factors, can influence biomass model accuracy (Temesgen et al. 2015) and incorporating these into equations may improve precision. However, models that include additional predictors (such as height and site covariates) can be more sensitive to measurement error and may perform poorly when applied outside the range of the original calibration data, reducing transferability. Using a single predictor, such as *DBH*, is therefore less complicated and more efficient, particularly in invasive species like Callery pear, where extremely high accuracy is not desired as for commercially valuable timber species. Also, models that include multiple variables, such as height and site, are often prone to error when applied outside the range of the original dataset (Chave et al. 2004). In addition, *DBH* alone has been shown to be a reliable and applicable predictor of biomass because it strongly correlates with tree size and is easy to measure in the field (Jenkins et al. 2003).

The performance of our log–log allometric model ($R^2 = 0.91$) is comparable to that reported by Boyce and Ocasio (2020), who obtained slightly higher model fits ($R^2 \approx 0.97$) using diameter at stump height (*DSH*) as the predictor. The small difference in model performance likely reflects differences in sample size, predictor definition, and environmental variability, as our model incorporates a broader range

of site conditions. At the same time, Callery pear commonly develops forked or multi-stem forms below breast height, meaning that a conventional *DBH* measurement is not always possible, which is why we restricted model development to single-stemmed individuals to ensure consistent *DBH* measurement and interpretation. For applications involving multi-stem Callery pear, alternative diameter definitions (e.g. diameter below the fork or other lower-stem measures) may be required to maintain consistency across divergent forms. Because invasion impacts scale with total biomass – affecting fuel loading, carbon stocks, removal costs, and site recovery – this *DBH*-based modelling approach provides a practical tool analogous to those used for commercially important species but tailored to an invasive tree for which no such tool previously existed for management and monitoring.

MC and C:N ratios offer additional insight into the physiological characteristics of Callery pear, though they play a secondary role relative to biomass modelling. *MC* differed among tissues, with branch material exhibiting lower mean *MC* than stems, while leaf and stem *MC* were similar; relationships between *MC* and *DBH* were tissue-dependent, with a modest decline in stem *MC* with increasing *DBH* but no detectable *DBH* association for leaves or branches, suggesting that tissue identity is the dominant axis of *MC* variation (Manwiller 1975; Sternberg, Shoshany 2001). Leaf and stem C:N ratios were lowest and highest, respectively, reflecting typical stoichiometric trade-offs between photosynthetic and structural tissues (Berg, McClaugherty 2014; Cornwell et al. 2008). While these traits alone do not determine decomposition or ecosystem impact, they provide valuable context for interpreting nutrient cycling, fuel characteristics, and potential effects of invasion intensity.

MC differed among tissues but was not affected by *DBH*, consistent with patterns in which *MC* is driven primarily by tissue anatomy and seasonal/environmental conditions rather than tree size (Henderson 1968; Manwiller 1975; Sternberg, Shoshany 2001). For trees with a *DBH* of approximately 15.24 cm in the southeastern United States, *MC* has been reported to range from 50.5% for white ash to 12% for sweetgum (Cassens 2007) and average around 50% for pine species (Manwiller 1975; Glass, Zelinka 2021). Callery pear, a hardwood species, exhibited an average *MC* of 42% in our study. This value is slightly lower than the regional average but

<https://doi.org/10.17221/49/2026-JFS>

because *MC* is strongly influenced by environmental and seasonal factors, the values reported here should be interpreted as baseline estimates rather than intrinsic species constants. They do, however, contribute to understanding fuel moisture characteristics and potential flammability, which may be relevant when considering management strategies involving fire (Keyes 2006; Coyle et al. 2021). Carbon–nitrogen ratios provide useful context for Callery pear litter quality, but predicting its ecosystem impacts requires consideration of invasion density, litter chemistry, and decomposition dynamics. Across tissues, Callery pear averaged a C:N ratio of 106.44, with leaves C:N closely matching previously reported measurements (≈ 36 ; Boyce 2022). Although C:N reflects nitrogen economy, decomposition and nutrient cycling depend on multiple interacting litter traits such as lignin, phenolics, and microclimate, rather than C:N alone (Berg, McClaugherty 2014; Cornwell et al. 2008). Recent evidence also indicates that Callery pear leaf tissues contain numerous unique secondary metabolites, especially flavones, suggesting that chemically mediated effects on soils and biotic communities may be important alongside C:N-based litter quality (Hartshorn 2025). For example, Chinese privet – another invasive plant in the same region with N-rich litter – can alter soil carbon storage, productivity, soil nitrate, and decomposer communities only when paired with dense stands and high litter inputs (Weand 2020; Bush et al. 2020). Hence, despite having leaf C:N values like privet and some native species, it can be concluded that Callery pear's ecosystem effects will hinge on invasion density, litter quantity and chemistry, and site conditions, rather than C:N alone (Boyce 2022; Zhang et al. 2008; Aubrey et al. 2012). Future work coupling litter chemistry (e.g. lignin:N, phenolics) with litterfall quantity and decomposition rates would be required to link Callery pear traits to ecosystem process changes (Berg, McClaugherty 2014; Cornwell et al. 2008).

Overall, the *DBH*-based equation developed here provides a practical first approximation for estimating aboveground biomass of single-stem Callery pear within the sampled *DBH* range (1.2–17.7 cm) and under conditions broadly like the six South Carolina sites sampled. However, the model should not be extrapolated uncritically to larger trees, multi-stem individuals, or regions outside the southeastern United States without additional validation.

Future studies should expand the calibration dataset across broader *DBH* ranges, geographic regions, invasion intensities, and stem architectures.

CONCLUSION

Overall, this study provides a comprehensive species-specific foundation for quantifying *AGB* of Callery pear, tissue traits (C:N ratios, nitrogen concentration, and moisture content) and develops species-specific allometric equations for predicting aboveground biomass (*AGB*). Although allometric equations are widely available for commercially important tree species, few exist for invasive trees such as Callery pear (Jenkins et al. 2003; Hulshof et al. 2015; McPherson et al. 2016). The *DBH*-based log-linear model developed here provides a practical approach for estimating *AGB* at landscape scales and can be applied to invasion monitoring, carbon accounting, biomass removal planning, and forest inventory applications. Because the model was developed using single-stem trees, caution is needed when applying it to multi-stem individuals. Future work should include multi-stemmed trees, expand the diameter range, and evaluate seasonal variation in tissue traits. Additional applications include carbon budgeting (Russell et al. 2015) and integrating *DBH*-based allometry with remote sensing for large-scale biomass estimation and invasion monitoring (Jucker et al. 2017). By advancing species-specific biomass estimation and highlighting key physiological traits, this study contributes to a more comprehensive understanding of Callery pear's ecological role and assisting land managers in evaluating biomass accumulation aimed at controlling and mitigating its spread.

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Received: June 15, 2026

Accepted: August 31, 2026

Published online: September 30, 2026