Biomass Allocation and Model Construction for Six Early-Summer Herb Species at Different Growth Stages in the Understory of a Broadleaf-Korean Pine Forest (Postprint)

Authors: Sun Yue, He Huaijiang, Li Liang, Song Caimin, Wang Fengjie, Xia Fucai

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Abstract

Early-summer herbaceous plants, as a group of dominant species in the understory of broadleaf-Korean pine forests, exert significant influence on understory herbaceous species diversity and biomass throughout the growing season, and research on their biomass allocation characteristics and biomass models at different growth stages contributes to understanding the survival strategies and carbon storage of these plants. This study examined six early-summer herbaceous species—Cardamine leucantha, Paris verticillata, Smilacina japonica, Meehania fargesii, Anisodus acutangulus, and Sanicula rubriflora—in the understory of broadleaf-Korean pine forests in the Jiaohe area of Jilin Province, observed and recorded their phenological periods from early April to late August, conducted regular sampling to analyze biomass allocation characteristics of various components and allometric relationships between above-ground and below-ground biomass across different growth stages, and developed five types of biomass models (simple linear, quadratic, exponential, power function, and logarithmic models) using plant height as the independent variable for both single-species and mixed-species scenarios, selecting optimal models for validation. The results indicated that the flowering period of the six early-summer herbaceous species generally began at the end of April and ended in mid-June, while the fruiting period began at the end of May and ended in mid-August, with substantial variation in the duration of flowering and fruiting periods among different species. During the growing season, plant height, biomass, and root-to-shoot ratio (R/S) exhibited significant changes with plant growth, though the trends were inconsistent. Biomass allocation among various components differed among species, with the proportion allocated to reproduction being relatively small, typically not exceeding 5%. All species showed significant allometric relationships between AGB and BGB ($P < 0.0001$), with allometric growth patterns (allometric exponent a   1). Optimal biomass models were selected based on R^2 and SEE, with the power function model being the most frequently used form, followed by quadratic and exponential models. All optimal models exhibited high R^2 values and low SEE, indicating good fit, with optimal models for AGB and TB performing better than those for BGB, and single-species models outperforming mixed-species models. Validation revealed that, except for the RMA of the mixed-species BGB model (30.679%) which slightly exceeded 30%, all models had RS, EE, and RMA values below 30% and P-values above 80%, demonstrating that the established optimal models can be used to estimate the biomass of early-summer herbaceous plants in the understory of broadleaf-Korean pine forests in this region.

Full Text

Preamble

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Biomass Allocation and Allometric Models of Six Early-Summer Herbs Under the Canopy of Broad-Leaved Korean Pine Forest During Different Growth Periods in Jiaohe, Jilin Province

Sun Yue[1], He Huaijiang[2], Li Liang[1], Song Caimin[3], Wang Fengjie[3], Xia Fucai[1]
[1]College of Forestry, Beihua University; Beijing Forestry University, Key Laboratory of Forest Resources and Ecosystem Processes, Beijing
[2]Jilin Jiaohe Forestry Experimental Area Administration Bureau

Abstract

Early-summer herbs represent a dominant component of the understory vegetation in broad-leaved Korean pine (*Pinus koraiensis*) forests and exert significant influence on herbaceous species diversity and biomass throughout the growing season. Investigating biomass allocation patterns and allometric models across different growth stages enhances understanding of these species' survival strategies and carbon storage capacity. This study examined six early-summer herbaceous species in the broad-leaved Korean pine forests of Jiaohe, Jilin Province: *Cardamine leucantha*, *Paris verticillata*, *Smilacina japonica*, *Meehania fargesii*, *Anisodus acutangulus*, and *Sanicula rubriflora*. Phenological observations were conducted from late April until the end of the growth period. We analyzed biomass allocation characteristics among different components during various growth stages and examined the relative growth relationships between aboveground and belowground biomass. Using plant height class as the independent variable, we developed single-species and mixed-species biomass models including linear, quadratic, and power functions, validating the optimal models. The flowering period for these six early-summer herbs generally began in early May and ended in late May, while the fruiting period started in late May and concluded in late June. Total biomass and root/shoot ratio (R/S) varied among species and across growth stages, though trends differed. All species exhibited significant allometric relationships between aboveground and belowground biomass, with power functions being the most commonly selected model form, followed by quadratic and exponential models. All optimal models showed high R^2 values (all <0.0001) and 1, indicating allometric rather than isometric growth. Single-species models consistently outperformed mixed-species models, with all validation P-values exceeding 0.05, demonstrating that the established optimal models can reliably estimate early-summer herb biomass in this region' s broad-leaved Korean pine forests.

Keywords: early-summer herbs; biomass allocation; root/shoot ratio (R/S); biomass model; allometric relationship

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Corresponding Author: E-mail: xfc0707@163.com

1. Study Area Overview

The study area is located within the Jiaohe Forestry Experimental Area Administration Bureau in Jilin Province (127°35 -127°51 E, 43°51 -44°05 N), covering 31,820 hectares. The region features a temperate continental mountain climate influenced by monsoons, with an average annual temperature of 3.8°C (ranging from -18.6°C in January to 21.7°C in July) and annual precipitation of 700–800 mm concentrated in June–August. Elevations range from 459 to 517 m. The terrain belongs to the Zhangguangcai Range of the Changbai Mountain system, characterized by fault-block landforms. Soils are forest dark brown earths rich in organic matter.

The vegetation belongs to the Changbai Mountain flora, with well-preserved broad-leaved Korean pine forests. The forest community exhibits distinct vertical stratification. Dominant tree species include *Pinus koraiensis*, *Fraxinus mandshurica*, *Quercus mongolica*, *Tilia amurensis*, *Acer mono*, *Juglans mandshurica*, *Ulmus laciniata*, *Populus ussuriensis*, *Acer barbinerve*, *Syringa reticulata*, *Lonicera maackii*, *Maackia amurensis*, and *Corylus mandshurica*. The understory is rich in herbaceous species, creating distinct seasonal landscapes. Common herbaceous plants include *Anemone amurensis*, *Anemone raddeana*, *Cardamine leucantha*, *Gagea lutea*, *Meehania fargesii*, *Paris verticillata*, *Anisodus acutangulus*, *Hylomecon japonicum*, *Lilium distichum*, *Smilacina japonica*, *Sanicula rubriflora*, *Aegopodium alpestre*, *Urtica fissa*, *Carex siderosticta*, and *Adonis* spp.

1. Sample Collection and Processing

We selected naturally growing populations of six early-summer herbaceous species in the natural broad-leaved Korean pine forest in Jiaohe: *Cardamine leucantha*, *Paris verticillata*, *Smilacina japonica*, *Meehania fargesii*, *Anisodus acutangulus*, and *Sanicula rubriflora*. For each species, we marked 30 representative, healthy individuals. Phenological observations were recorded from late April until the end of the growth period. Flowering onset was defined when 50% of observed individuals showed open flowers; flowering cessation when 50% of flowers had withered. Fruiting periods were recorded using the same methodology. Special attention was paid to excavating complete perennial root systems including rhizomes.

Sampling was conducted at different growth stages, with sample sizes varying by species and stage (detailed in Table 1). After collection, root soil was washed clean. Plant height was measured with a steel ruler from root collar to the tallest point. Whole-plant harvest method was employed: plants were separated into roots, stems, leaves, flowers, and fruits, then oven-dried at 80°C to constant weight (±0.0001 g). Component biomasses were summed to obtain total biomass (TB).

2. Data Processing and Analysis

We analyzed the allometric relationship between aboveground biomass (AGB) and belowground biomass (BGB) using the model:

$$Y = \beta X^{\alpha}$$

After logarithmic transformation:

$$\lg BGB = \lg \beta + \alpha \lg AGB$$

where α is the allometric scaling exponent and β is a constant. Isometric growth occurs when $\alpha = 1$; allometric growth when $\alpha \neq 1$. We determined growth type by examining whether the 95% confidence interval of α contained 1. To account for biomass variation due to age, microclimate, and phenology among plants of similar height, we used mean biomass values for each height class (±2 cm for *Cardamine leucantha*, *Meehania fargesii*, and *Sanicula rubriflora*; ±1 cm for *Paris verticillata*, *Smilacina japonica*, and *Anisodus acutangulus*).

For model construction, we randomly selected 70% of individuals per species as training data and 30% as validation data, distributed proportionally across height classes. Using height class as the independent variable, we developed biomass estimation models with five equation forms:

1. Linear: $y = ax + b$
2. Quadratic: $y = ax^2 + bx + c$

3. Power: $y = ax^b$
4. Exponential: $y = ae^{bx}$
5. Hyperbolic: $y = a + b/x$

where y represents component biomass, x is height class, and a, b, c are parameters. Model accuracy was assessed using relative error (RE), mean relative error (MRE), mean absolute relative error (MARE), and prediction precision (P):

$$RE = \frac{y_i - \hat{y}_i}{\hat{y}_i} \times 100\%$$

$$MRE = \frac{1}{n}\sum_{i=1}^{n} RE_i$$

$$MARE = \frac{1}{n}\sum_{i=1}^{n} |RE_i|$$

$$P = 1 - \frac{t_\alpha \times \sqrt{\sum(y_i - \hat{y}_i)^2/n}}{\bar{y}}$$

where y_i and $\hat{y}_i$ are observed and predicted biomasses for sample i, n is sample size, and t_α is the t-distribution value at significance level α (set at 0.001). Data processing used Excel 2013 and SigmaPlot 10.0; statistical analysis used R-3.2.3.

2. Results and Analysis

2.1 Phenological Periods of Flowering and Fruiting

The six early-summer herbs showed distinct phenological patterns (Figure 1). *Sanicula rubriflora* flowered earliest (late April), while *Paris verticillata* flowered latest (mid-May). Flowering duration varied significantly: *Sanicula rubriflora* had the longest period (49 days), whereas *Meehania fargesii* and *Anisodus acutangulus* had the shortest (22 days). Fruiting initiation varied markedly among species, with *Anisodus acutangulus* fruiting earliest and *Paris verticillata* latest. Fruiting duration ranged from 15 days in *Meehania fargesii* to 104 days in *Smilacina japonica*. The complete reproductive period was shortest in *Meehania fargesii* (37 days) and longest in *Smilacina japonica*.

[Figure 1: see original paper]

2.2 Biomass and Growth Dynamics Across Growth Periods

Throughout the growing season, plant height, biomass, and root/shoot ratio (R/S) showed substantial variation (Figure 2). Maximum plant height at growth peak reached 6–87.6 cm, with biomass at growth 末期 reaching up to 100 times initial values. R/S ratios varied by an order of magnitude. All six species exhibited increasing height during early growth. *Sanicula rubriflora* peaked in height by late May then declined significantly, while other species showed slight height reductions after maximum growth. Height growth rates peaked early then declined, indicating rapid height extension before canopy closure to maximize light capture. After canopy closure, light became limiting and height growth ceased as plants shifted to reproductive phases and senescence.

Total biomass trends mirrored height patterns, peaking then declining. *Sanicula rubriflora* achieved the highest individual biomass, while *Paris verticillata* had the lowest. Reproductive organ biomass showed species-specific patterns: *Sanicula rubriflora* accumulated reproductive biomass earliest, peaking in late May; *Cardamine leucantha* showed similar but more rapid fruit maturation; *Smilacina japonica* maintained the longest reproductive period with slow initial increase followed by significant late-season growth; *Paris verticillata* initiated reproductive allocation latest and shortest, completing reproduction rapidly to minimize disturbance exposure.

R/S ratios varied by species and stage. *Cardamine leucantha*, *Anisodus acutangulus*, and *Meehania fargesii* showed highest R/S initially, decreasing to stability. *Smilacina japonica* and *Paris verticillata* showed opposite trends, with R/S increasing through the season due to rhizome development continuing after shoot growth ceased.

[Figure 2: see original paper]

2.3 Biomass Allocation and Allometric Relationships

Reproductive biomass allocation remained low (<5%) throughout the growth period for all species, with vegetative and belowground components dominating. Allocation patterns varied among species and across stages. Most species showed initial low vegetative allocation increasing to 60–80% during reproductive phases. Belowground allocation showed inverse patterns to aboveground vegetative parts.

All six species exhibited significant allometric relationships between aboveground and belowground biomass (Table 2). *Cardamine leucantha*, *Anisodus acutangulus*, and *Sanicula rubriflora* had scaling exponents < 1 (95% CI upper bounds <1), indicating slower belowground than aboveground growth. *Paris verticillata* and *Smilacina japonica* had > 1 (95% CI lower bounds >1), reflecting faster belowground growth due to rhizome development. All relationships were highly significant ($P < 0.0001$).

4. Biomass Model Construction and Optimal Model Validation

Using height class as the predictor, we developed estimation models for AGB, BGB, and TB. Model selection prioritized high R^2 values and biological realism. Optimal models and parameters are presented in Table 3. Power functions were most frequently selected (9 of 15 models), followed by exponential and quadratic forms. Single-species models consistently outperformed mixed-species models, with R^2 values >0.90 for most components. Mixed-species models showed lower R^2 (0.443–0.977), particularly for belowground biomass, likely due to interspecific differences in growth rates and measurement uncertainties.

Model validation using reserved samples showed all equations had relative errors ranging from -12.459% to 6.180%, MARE from 10.470% to 30.697%, and prediction precision $P > 0.05$ (Table 4). All models met validation criteria (MARE <30%), though mixed-species models showed higher errors. The mixed-species model for belowground biomass had the highest MARE (30.679%) but remained acceptable.

1. Biomass Allocation and Relative Growth Relationships

Biomass allocation strategies represent evolutionary adaptations to environmental conditions, enabling plants to maximize resource utilization under varying circumstances. However, allocation patterns differ substantially among species and growth stages. Northeastern broad-leaved Korean pine forest understory herbs typically allocate more biomass aboveground to compete for limited light before canopy closure. Our results show that *Cardamine leucantha*, *Anisodus acutangulus*, and *Sanicula rubriflora* initially had R/S > 1, decreasing through the season as plants prioritized light acquisition then stabilized allocation. In contrast, *Paris verticillata* and *Smilacina japonica*, both rhizomatous perennials, showed increasing R/S over time as rhizomes continued growing after canopy closure, storing resources for vegetative propagation.

Allometric theory and vascular network models predict power-law relationships between plant organ biomasses. While global studies suggest isometric scaling (= 1) across diverse plants, our findings show 1 for all species, indicating allometric growth. This discrepancy likely reflects our focus on complete ontogenetic trajectories from seedling to maturity, whereas many global syntheses emphasize mature individuals. The dynamic nature of scaling exponents across growth stages warrants further investigation into stage-specific allometries.

2. Biomass Model Establishment and Testing

Biomass modeling based on easily measured variables provides accurate assessment of understory carbon pools. For herbaceous plants, height is a practical predictor variable. While some studies use basal diameter and crown width, these were unsuitable here due to small diameters and high measurement variability. Using height class as the sole predictor yielded robust single-species models ($R^2 > 0.90$) for all biomass components, consistent with previous herbaceous biomass studies.

Model form selection varied by species, with power functions most common—a widely applied approach for both woody and herbaceous vegetation. Single-species models consistently outperformed mixed-species versions due to interspecific differences in growth rates and allometric parameters. Belowground biomass models showed lower precision than aboveground or total biomass models, likely reflecting root loss during excavation and cleaning—a common challenge in root biomass studies.

All validated models met acceptance criteria (MARE <30%, $P > 0.05$), confirming their applicability for estimating early-summer herb biomass in broad-leaved Korean pine forests. However, these models require validation before application to other forest types or non-forest conditions, as they were developed specifically for this ecosystem and species assemblage.

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Note: Figure translations are in progress. See original paper for figures.