# Allometric Growth Laws of Salix psammophila Biomass Under Different Site Conditions in the Mu Us Sandy Land (Postprint)

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## Abstract

To investigate the adaptive strategies of *Salix psammophila* to different sandy desert environmental conditions from the perspective of biomass accumulation and allocation, reveal the primary environmental factors influencing biomass allocation in *S. psammophila*, and provide a reference for population stability construction and sustainable management of *S. psammophila*, we selected *S. psammophila* forests in four site types (windward slope, leeward slope, interdune lowland, and flat sandy land) as study objects. We measured the basal diameter, length, and stem and leaf biomass of representative clustered branches in each sample plot, and established allometric equations for stem and leaf biomass against basal diameter and branch length using standardized major axis regression to elucidate the dependence of stem and leaf biomass accumulation and allocation on individual size at the clustered branch scale. Furthermore, through the principal axis shift method, we examined differences in stem and leaf biomass allometric equations among different site types, thereby exploring the influence of environmental conditions on biomass accumulation and allocation in *S. psammophila*. The results showed that: (1) With increasing individual size of clustered branches, the stem biomass accumulation rate was higher than the leaf biomass accumulation rate, and this pattern was consistent across all site types; (2) The allocation of stem and leaf biomass in *S. psammophila* clustered branches differed significantly among site types, with the proportion of leaf biomass to total clustered branch biomass on dunes (windward and leeward slopes) being significantly higher than that in interdune lowlands and flat sandy lands ($P<0.05$); (3) The main soil factor causing differences in biomass and its allocation among site types was soil water content, wherein whole-profile water content (0–100 cm) was significantly correlated with clustered branch biomass ($P<0.01$), and deep soil water content (60–100 cm) was significantly correlated with aboveground biomass allocation of clustered branches. Biomass accumulation and allocation in *S. psammophila* showed significant differences among site types, with deep soil water content having a more significant effect on biomass allocation than whole-profile soil water content. Based on these results, appropriate artificial interventions can be implemented in the future to meet the water requirements for *S. psammophila* growth, thereby achieving stable development of *S. psammophila* plantation populations.

## Full Text

## Biomass Allocation and Allometric Growth Patterns of *Salix psammophila* Under Different Site Conditions in the Mu Us Sandy Land

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### Abstract

This study investigated the adaptive strategies of *Salix psammophila* to different sandy land environmental conditions from the perspective of biomass accumulation and allocation, aiming to identify the main environmental factors influencing biomass distribution and provide references for population stability construction and sustainable management. Natural *S. psammophila* stands on four typical site types—windward slope, leeward slope, interdune land, and flat sand land—were selected as study objects. Morphological parameters including basal diameter, branch length, and stem and leaf biomass of representative individuals were measured. Standardized major axis regression was used to establish allometric equations relating stem and leaf biomass to basal diameter and branch length, clarifying the dependence of biomass accumulation and allocation on individual size at the branch cluster scale. Further, the method of axis shift testing was employed to examine differences in stem-leaf biomass allometric relationships across site types, thereby exploring how environmental conditions affect biomass accumulation and allocation. Results showed that: (1) With increasing branch size, the accumulation rate of stem biomass in *S. psammophila* exceeded that of leaf biomass, a pattern consistent across all site types. (2) Biomass allocation between stems and leaves differed significantly among site types, with the proportion of leaf biomass to total branch biomass being significantly higher on dunes (windward and leeward slopes) than in interdune and flat sand lands ($P < 0.05$). (3) The primary soil factor causing site-specific differences in biomass and its allocation was soil moisture content. Whole-profile moisture content (0–100 cm) was significantly correlated with branch biomass ($P < 0.01$), while deep-layer moisture content (60–100 cm) was significantly correlated with aboveground biomass allocation. The biomass accumulation and allocation of *S. psammophila* showed significant variation among site types, with deep soil moisture having a more pronounced effect on biomass allocation than whole-profile moisture. Based on these findings, appropriate artificial interventions can be implemented in the future to meet the water requirements for *S. psammophila* growth, thereby achieving stable development of plantation populations.

**Keywords:** Mu Us Sandy Land; *Salix psammophila*; biomass allocation; site type; allometric growth

## 1 Introduction

The coordinated development of different plant organs is a crucial life-history strategy, with energy and material allocation among organs influenced by various environmental conditions such as light, temperature, water, and nutrient availability. According to the functional equilibrium hypothesis, when a particular resource becomes limiting, plants prioritize the allocation of metabolic products to organs that can acquire the limiting resource. For instance, when light is limiting, biomass is preferentially allocated to branches and leaves, whereas when nutrients or water are limiting, allocation favors roots. Allometric growth theory provides an important framework for studying biomass allocation, positing that biomass distribution is fundamentally constrained by individual size, with different organs exhibiting allometric relationships in biomass accumulation. If the allometric exponent $\alpha = 1$, growth is isometric; if $\alpha \neq 1$, growth is allometric, indicating differential scaling between organs. Environmental variation can alter these allometric relationships, with changes in the allometric exponent reflecting adaptive adjustments in biomass allocation patterns.

Desertified regions feature diverse site types with strong spatial heterogeneity in environmental conditions at local scales. Windward slopes experience intense wind erosion, leeward slopes suffer severe sand burial, and interdune lands often exhibit salinization characteristics. Whether these habitat differences affect biomass allocation patterns remains to be investigated. While previous studies have extensively explored trade-offs between above- and below-ground biomass and between reproductive and vegetative biomass in desert plants, the relationship between aboveground leaf (photosynthetic) and stem (mechanical support and hydraulic conduit) biomass has received limited attention, hindering a comprehensive understanding of desert plant environmental adaptation.

*Salix psammophila* is a dominant shrub species in the Mu Us Sandy Land, characterized by wind resistance, drought and salt tolerance, rapid growth, extensive root systems, and strong sand-fixing capacity. It is widely distributed across various landform types in sandy regions and serves as an excellent species for windbreak and sand fixation, as well as a typical energy crop in sandy areas. The aboveground portion of *S. psammophila* consists of clustered branches arising from rhizome tillering. The accumulation and allocation relationships of these branch clusters significantly influence windbreak efficacy and biomass resource development. Previous research has examined the effects of sandy land environments and stand density on *S. psammophila* biomass production, but studies on inter-organ biomass allocation patterns and responses to environmental factors remain scarce.

This study analyzed the size characteristics of branch clusters and the patterns of stem and leaf biomass accumulation and allocation in relation to size across different site types in the Mu Us Sandy Land. Combined with soil factor surveys, we established relationships between branch cluster biomass accumulation/allocation and environmental factors to reveal the adaptive regulatory mechanisms of *S. psammophila* from a biomass allocation perspective. This research not only enriches the data foundation for studies on biomass allocation and adaptive strategies of psammophytic plants but also provides theoretical support for the management and utilization of *S. psammophila* forests in the Mu Us Sandy Land.

### 1.1 Study Area Overview

The study was conducted at the Ningxia Yanchi Mu Us Sandy Land Ecosystem National Positioning Observation and Research Station (37.68°–37.73°N, 107.20°–107.26°E) operated by the School of Soil and Water Conservation, Beijing Forestry University. Located on the southern edge of the Mu Us Sandy Land, the region experiences a typical temperate continental monsoon climate. Influenced by the prevailing westerly circulation, the climate is arid with low rainfall, strong winds, abundant sand, and intense evaporation. The frost-free period averages 128 days, with a mean annual wind speed of 2.8 $m \cdot s^{-1}$, annual precipitation of 275 mm, mean annual evaporation of 1273.31 mm, and average annual gale days of 45.8 days and sandstorm days of 20.6 days. The landscape is dominated by alternating dunes and interdune lands, with loose aeolian sandy soil as the primary soil type. The vegetation is dominated by *Artemisia ordosica*, *Salix psammophila*, and *Caragana korshinskii*, with *S. psammophila* having the widest distribution. *S. psammophila* exhibits strong tolerance to drought, cold, high temperature, sand burial, and wind erosion, and can rapidly expand in mobile sandy lands due to its extensive root system, making it the most widely distributed suitable shrub in the semi-arid Mu Us Sandy Land.

### 1.2 Experimental Design and Measurements

At the end of the 2023 growing season, we selected four natural dune vegetation sites where *S. psammophila* was the constructive species. The sites were established in 2013 through artificial cutting propagation and had not experienced subsequent human disturbance. Each dune site was divided into four typical site types: windward slope, leeward slope, interdune land, and flat sand land (flat terrain distant from dunes). Three 20 m × 20 m plots were established for each site type. All *S. psammophila* shrubs in each plot were measured for height and crown width, and the number of branch clusters was recorded, totaling 450 shrubs. The average shrub density was $450 \pm 50$ plants $\cdot$ hm$^{-2}$, with an average crown width of $8.91 \pm 0.45$ m and average height of $3.15 \pm 0.37$ m.

Based on plot survey data, standard sample trees were selected using a grading method, and the harvest method was employed to measure biomass. During harvesting, the basal diameter (D) and branch length (L) of all branch clusters on each shrub were measured. Stems and leaves were placed in separate kraft paper bags, transported to the laboratory, and oven-dried at 75°C to constant weight (precision 0.01 g) to obtain stem biomass (Bs), leaf biomass (Bl), and total biomass (Bt).

To prevent data errors from one-time sampling, soil sampling was conducted once before and after rainfall events. In each plot, a five-point sampling method was used to collect soil samples with a soil auger at depth intervals of 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, and 80–100 cm. A total of 75 soil samples were collected to determine soil moisture content and available nitrogen and phosphorus concentrations.

### 1.3 Data Processing

One-way ANOVA was used to analyze differences in branch cluster basal diameter, branch length, morphological characteristics, and biomass among different topographies. The allometric power function model was employed to establish relationships between organ biomass and basal diameter, revealing biomass accumulation patterns during individual growth, and between stem and leaf biomass to clarify allocation patterns. The allometric model takes the form $Y = \beta M\hat{}\alpha$, where parameters were estimated using Standardized Major Axis (SMA) regression to obtain the allometric exponent $\alpha$ and constant $\beta$. In this model, Y and M represent the two variables used. If $\alpha = 1$, Y and M exhibit isometric growth; if $\alpha \neq 1$, growth is allometric. When $\alpha > 1$, Y grows faster than M; when $\alpha < 1$, Y grows slower than M.

Based on the allometric analysis, axis shift testing was performed on the allometric exponent $\alpha$ across different site types to examine differences in biomass accumulation and allocation [Figure 1: see original paper]. Pearson correlation analysis was used to assess relationships between environmental factors and branch cluster biomass and the allometric exponent $\alpha$, identifying factors influencing biomass accumulation and inter-organ allocation.

Data were processed using SPSS Statistics 22 for ANOVA and correlation analysis. SMA regression, axis shift testing, and isometry testing were conducted using R 3.5.1 with the SMATR package (R Development Core Team, 2022).

## 2 Results

### 2.1 Morphological Parameters and Biomass Characteristics of *S. psammophila* Branch Clusters

The mean basal diameter of branch clusters varied among the four site types: windward slope (1.57 ± 0.73 cm), leeward slope (1.67 ± 0.91 cm), interdune land (1.50 ± 0.803 cm), and flat sand land (1.57 ± 0.86 cm), with no significant differences among them ($P > 0.05$). The basal diameter data were concentrated between 1.0–2.0 cm, with windward and leeward slopes showing left-skewed distributions [Figure 1: see original paper].

Significant differences were observed in mean branch length among site types ($P < 0.05$). Flat sand land had the longest branches (292.52 ± 102.89 cm), while windward slopes had the shortest (240.77 ± 53.13 cm), followed by leeward slopes (281.18 ± 84.16 cm) and interdune land (241.25 ± 74.45 cm). Branch length showed the greatest variability in flat sand land, with approximately 50% of branches ranging 200–400 cm, while windward slope branches were most concentrated, with approximately 60% ranging 200–300 cm. Branch length data followed normal distributions across all site types [Figure 1: see original paper].

Stem and leaf biomass data for branch clusters exhibited significant left-skewed distributions across all site types, indicating concentrated distribution in low-value ranges [Figure 2: see original paper].

### 2.2 Aboveground Biomass Accumulation and Allocation Patterns Across Site Types

Stem biomass, leaf biomass, and total biomass accumulated significantly with increasing basal diameter [Figure 3: see original paper]. Power functions fitted to these relationships yielded coefficients of determination $R^2 > 0.59$ for all site types, indicating good model performance. Axis shift testing revealed significant differences in the power function exponents among site types ($P < 0.05$). The allometric exponent $\alpha$ for total biomass vs. basal diameter was significantly greater on leeward slopes than on windward slopes and interdune land ($P < 0.05$), while no significant differences were found for stem biomass vs. basal diameter ($P > 0.05$). The leaf biomass vs. basal diameter exponent $\alpha$ was also significantly higher on leeward slopes than on windward slopes and interdune land ($P < 0.05$) .

These results demonstrate that environmental conditions affect leaf biomass accumulation rates, thereby influencing total aboveground biomass accumulation rates. As basal diameter increased, the proportion of biomass allocated to stems gradually rose. For interdune land, stem biomass allocation increased from 79.4% to 92.0% as basal diameter grew from 0.59 cm to 3.01 cm, an increase of 12.6 percentage points. Similar increases occurred on windward slopes, leeward slopes, and flat sand land (average increase of 15.9%). Concurrently, leaf biomass allocation proportion decreased correspondingly. This indicates that while stem biomass allocation increases with branch growth across all environments, the magnitude of this increase varies among site types, reflecting adaptive adjustments in biomass allocation to different environmental conditions [Figure 4: see original paper].

### 2.3 Allometric Growth Between Organs Across Site Types

The allometric relationship between stem and leaf biomass is shown in [Figure 5: see original paper]. Axis shift testing revealed significant differences in the stem-leaf biomass allometric exponent $\alpha$ among the four site types ($P < 0.01$), indicating altered biomass allocation patterns across environments .

On windward and leeward slopes, leaf and stem biomass exhibited isometric growth ($\alpha$  1, $P > 0.05$), suggesting stable scaling relationships during plant growth. In contrast, on interdune land and flat sand land, the stem-leaf allometric exponent was significantly less than 1 ($P < 0.01$), indicating faster stem biomass growth relative to leaf biomass.

Axis shift comparisons showed that leaf biomass allocation was significantly higher on dune slopes than in interdune and flat sand lands.

### 2.4 Effects of Soil Factors on Biomass and Allocation

Soil moisture content varied significantly among site types ($P < 0.05$), while available nutrient content showed no significant differences ($P > 0.05$). In the 0–60 cm soil layer, moisture content was higher in flat sand land and windward slopes than in leeward slopes and interdune land ($P < 0.05$). In the 60–100 cm layer, interdune land and flat sand land had significantly lower moisture content than dune slopes ($P < 0.01$). These moisture patterns, which differ from traditional understanding of dune moisture distribution, were confirmed through repeated sampling and are not experimental errors. The lower deep soil moisture in interdune land and flat sand land may be related to high vegetation cover and developed biological soil crusts that intercept precipitation, limiting deep soil water recharge [Figure 6: see original paper].

Correlation analysis revealed no significant relationships between available nutrient content and the stem-leaf allometric exponent $\alpha$, indicating that nutrient availability did not significantly influence allocation patterns. However, whole-profile soil moisture and deep-layer moisture were significantly correlated with the stem-leaf allometric exponent $\alpha$. While whole-profile moisture determined overall plant biomass, deep-layer moisture directly affected biomass allocation strategies, with higher deep moisture corresponding to greater leaf biomass allocation proportions .

# 3 Discussion

### 3.1 Biomass Allocation Patterns During Branch Cluster Development

In specific environments, individual size is the primary internal factor constraining biomass accumulation and allocation. As *S. psammophila* branch clusters increase in size, biomass accumulates in both stem and leaf components, with the proportion allocated to stems increasing while that to leaves decreases [Figure 4: see original paper]. This pattern aligns with findings from studies on *S. psammophila* allometric relationships and population dynamics. The underlying mechanism may involve reduced hydraulic resistance in smaller individuals, allowing unrestricted leaf expansion, whereas larger individuals face increased water potential gradients from roots to leaves, making water transport efficiency the primary growth-limiting factor. This leads to increased resource allocation to stem tissue for enhanced water transport capacity. This interpretation is supported by the allometric relationship between branch length and basal diameter (L-D), where the exponent $\alpha = 0.42$ indicates that radial growth rate far exceeds length growth rate . This suggests that as plants develop, radial growth accelerates to improve water transport efficiency while length growth slows to minimize hydraulic resistance, explaining the increasing stem biomass proportion. This fundamental pattern of decreasing leaf biomass and increasing stem biomass with individual growth applies across all site types.

### 3.2 Site Type Differences in Biomass and Allocation Patterns

In natural habitats, resource availability varies among site types. Plants adjust inter-organ biomass allocation to respond to environmental heterogeneity. Allometric analysis of allocation plasticity during growth provides insights into adaptive mechanisms. This study found that the stem-leaf allometric exponent $\alpha$ was significantly lower in interdune land and flat sand land than on dune slopes , demonstrating plasticity in organ biomass scaling relationships with environmental variation, consistent with research on other desert shrubs.

Soil moisture content explained these differences in the stem-leaf allometric exponent $\alpha$. Deep soil moisture (60–100 cm) varied significantly among site types [Figure 6: see original paper] and was significantly positively correlated with the stem-leaf allometric exponent $\alpha$ . Higher deep moisture increased leaf biomass allocation proportion, while lower moisture, as observed in interdune land and flat sand land, led to reduced leaf allocation and increased stem allocation to enhance water transport capacity. The lower deep moisture in interdune land and flat sand land may be attributed to high vegetation cover and biological soil crusts that intercept precipitation, limiting deep soil water recharge. Since *S. psammophila* roots are primarily distributed in the 60–100 cm layer, reduced deep moisture directly affects water uptake, resulting in lower leaf biomass proportions compared to dune slopes.

Previous studies have identified soil moisture as the dominant factor affecting biomass accumulation in desert shrubs, and this research confirms the specific influence of layered moisture on biomass allocation. Therefore, soil moisture is the primary factor controlling *S. psammophila* plantation growth and biomass allocation in the Mu Us Sandy Land. Poorer moisture conditions lead to lower primary productivity and reduced investment in photosynthetic leaf biomass, with greater allocation to tissues involved in water absorption and transport. Based on these findings, artificial interventions such as adjusting stand age structure and increasing soil infiltration could improve site moisture conditions and optimize population growth.

## 4 Conclusion

1) During individual development, *S. psammophila* branch clusters exhibit faster stem biomass accumulation than leaf biomass accumulation.
2) Biomass allocation patterns vary significantly among site types, with higher leaf biomass proportions on dunes compared to interdune land and flat sand land.
3) Soil moisture content is the primary factor influencing biomass allocation, with deep soil moisture (60–100 cm) having the most significant effect on allocation patterns.

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