# Effects of Population Density on Morphological Characteristics and Allometric Growth of Corispermum macrocarpum Postprint

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## Abstract

To reveal the allometric relationships between population density and plant morphological characteristics and organ biomass, and to elucidate the adaptive strategies of plants during the restoration of degraded land, this study used *Corispermum macrocarpum* as the experimental material and employed allometric analysis methods to investigate the effects of population density on its morphological characteristics, biomass allocation, and allometric growth. The results demonstrated that population density exerted significant effects on the architectural construction of *C. macrocarpum*. With increasing density, plant height of *C. macrocarpum* showed a decreasing trend, while both branch number and branch length decreased significantly. The biomass of all organs in *C. macrocarpum* decreased significantly with increasing density. With increasing density, biomass allocation to stems and reproductive organs showed a decreasing trend, whereas biomass allocation to roots and leaves showed an increasing trend. This pattern is consistent with scenarios of water, nutrient, and light resource limitation in optimal allocation theory. Density had a significant effect on the allometric growth between plant height and root biomass in *C. macrocarpum*, and exerted highly significant effects on the allometric exponent between plant height and organ biomass as well as on individual size. The effects of density on root:shoot, leaf:root, and reproductive organ:root biomass ratios belonged to apparent plasticity, whereas the effects on root:stem, stem:shoot, leaf:other organs, and reproductive organ:other organs biomass ratios belonged to true plasticity, indicating that density altered the plant architectural development system of *C. macrocarpum* and affected allometric growth among organs, thereby trading off organ biomass allocation to complete the life history.

## Full Text

## Preamble

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**Influence of Population Density on Morphological Traits and Allometric Growth of *Corispermum macrocarpum***

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## Abstract

This study aimed to reveal the allometric relationships between population density, plant morphological characteristics, and organ biomass allocation, and to elucidate the adaptive strategies of plants during the restoration of degraded land. Using allometric analysis, we investigated the effects of population density on morphological traits, biomass distribution, and allometric growth in *Corispermum macrocarpum*. Our results showed that density significantly affected plant architecture in *C. macrocarpum*. With increasing density, plant height decreased, while branch number and length were significantly reduced. Total organ biomass decreased significantly with density. Biomass allocation to stems and reproductive organs decreased, whereas allocation to roots and leaves increased. These findings are consistent with optimal allocation theory predictions under conditions of limited water, nutrients, and light resources. Density had highly significant effects on the allometric exponents and individual size between plant height and organ biomass. The allometric relationship between height and root biomass was significantly affected by density. The influence on root biomass represented apparent plasticity, while effects on other organs and between reproductive and other organ biomass represented true plasticity. Density altered the ontogenetic system of plant architecture in *C. macrocarpum*, affected allometric relationships among organs, and resulted in trade-offs in biomass allocation to complete the life history.

**Keywords:** allometry; phenotypic plasticity; biomass allocation; population density; *Corispermum macrocarpum*

## 1. Study Area Overview

The study area was located at the Naiman Desertification Research Station of the Chinese Academy of Sciences in Naiman Banner, Tongliao City, Inner Mongolia, situated in the south-central Horqin Sandy Land (120°19′–121°35′E, 42°14′–43°32′N). The region has a temperate semi-arid continental monsoon climate with distinct seasonal variations. Elevation is 360 m, mean annual precipitation is 365 mm (concentrated in June–August), annual evaporation is 1935.4 mm, mean annual temperature is 6.3°C, and the frost-free period is approximately 150 days. The zonal vegetation is temperate semi-arid steppe, but severe desertification has replaced it with psammophytic vegetation. Dominant species include *Agriophyllum squarrosum*, *Setaria viridis*, *Chenopodium acuminatum*, *Corispermum macrocarpum*, and *Potentilla bifurca*. The soil type is sandy chestnut soil, with extensive sandy substrate distribution and strong wind activity (average wind speed 3.5 m/s).

## 2. Experimental Design

Within the Naiman Desertification Research Station, we selected uniform sandy grassland and established experimental plots by artificial seeding. Based on the natural density range of *C. macrocarpum* populations during desertified land restoration, we established four density treatments in 3 m × 3 m plots: D1) 16 plants/m$^2$; D2) 44.4 plants/m$^2$; D3) 100 plants/m$^2$; and D4) 400 plants/m$^2$. Each treatment had three replicates. Throughout the growing season, weeds were manually removed weekly, with no other human interference.

Destructive sampling was conducted on August 15, 2016. To avoid sampling effects, we randomly sampled in previously unsampled areas each time. Five plants were randomly selected from each plot, washed clean to obtain intact root systems, and separated into roots, stems, leaves, and reproductive organs (flowers and fruits). Plant height and branch characteristics were measured. All samples were oven-dried at 75°C to constant weight and weighed to determine biomass allocation to each organ (relative biomass).

## 3. Data Analysis

We used the classical allometric equation $Y = \beta X^{\alpha}$, where $Y$ is the organ attribute being studied, $X$ is individual plant size (or another organ attribute), $\alpha$ is the allometric exponent, and $\beta$ is the allometric constant (Y-intercept). To determine allometric exponents, we fitted log-transformed data using reduced major axis regression (RMA), which minimizes variable bias on regression coefficients. The regression coefficient $r$ is the correlation coefficient. Significance testing used F-tests. We used SPSS 17.0 for ANOVA to compare organ biomass characteristics and allocation plasticity among treatments, with LSD tests for mean comparisons. SMA regression was performed using SMATR software. Significance levels were: ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

## 2. Results and Analysis

### 2.1 Effects of Density on Allometric Relationships

This analysis focused on allometric exponents, constants, and changes in individual size ($X$), comparing exponents with the 3/4 scaling expectation.

#### 2.1.1 Effects of Population Density on Allometric Growth Between Height and Organ Biomass in *C. macrocarpum*

Allometric analysis revealed that population density significantly affected the allometric relationship between height and root biomass in *C. macrocarpum* ($P < 0.05$), but had no significant effect on allometric relationships between height and reproductive organs or height and stem biomass ($P > 0.05$). Density had highly significant effects on allometric exponents and individual size between plant height and organ biomass ($P < 0.01$). Height, reproductive organ biomass, and aboveground biomass increased significantly with density ($P < 0.001$). Significant differences existed among D1-D3 densities for these traits, while differences between D1-D4 were not significant for reproductive organ biomass. Aboveground biomass showed significant differences between D1-D2 and D2-D3, with other density pairs being non-significant. Plant height decreased with increasing density ($F = 70.602, P < 0.001$). Allometric coefficients between height and reproductive biomass showed no significant differences among densities, while those between height and root biomass differed significantly between D2-D4 and D3-D4 ($P < 0.01$), and highly significantly between D1-D4 ($P < 0.001$).

#### 2.1.2 Effects of Population Density on Reproductive Allocation and Its Allometric Relationship with Other Organs

Reproductive organ biomass in *C. macrocarpum* decreased significantly with density, showing a highly significant negative correlation ($F = 43.584, P < 0.001$). Highly significant differences existed among all density treatments. Reproductive allocation also decreased with density, showing a highly significant negative correlation. Density had highly significant effects on allometric exponents and individual size between reproductive organs and other organs, except for reproductive organ vs. stem biomass and reproductive organ vs. leaf biomass, where effects were not significant ($P > 0.05$). Allometric exponents for reproductive organ vs. stem and reproductive organ vs. leaf biomass did not change with density. Reproductive organ biomass in D1 was significantly higher than in D2-D4, with no significant differences among D2-D4.

#### 2.1.3 Effects of Population Density on Leaf Biomass Allocation and Allometric Relationships with Other Organs

Leaf biomass allocation reflects plant strategies for responding to environmental changes throughout growth. With increasing density, leaf biomass in *C.*

*macrocarpum* decreased, showing a highly significant negative correlation ($F = 9.765, P < 0.001$). Leaf biomass allocation increased with density, showing a highly significant positive correlation. D1 had significantly lower leaf biomass allocation than D2-D4, with no significant differences among D2-D4. Density had highly significant effects on allometric exponents and individual size between leaf biomass and other organs, except for leaf vs. root biomass where the effect was not significant ($F = 0.079, P > 0.05$). Stem biomass increased significantly with density ($F = 6.890, P < 0.001$), showing a highly significant positive correlation, while root biomass did not change with density.

#### 2.1.4 Effects of Population Density on Stem Biomass Allocation and Allometric Relationships with Aboveground Biomass

As environmental conditions change, plant organs adapt significantly. Stems transport nutrients and water while supporting leaves and reproductive organs, directly determining spatial distribution of organs. Stem biomass in *C. macrocarpum* decreased significantly with density ($F = 47.554, P < 0.001$). Stem biomass allocation decreased with density, showing a significant negative correlation ($F = 3.148, P < 0.05$). D1 had significantly higher stem biomass allocation than other densities. Density had highly significant effects on allometric growth and individual size between stem and aboveground biomass, but no significant effect on allometric exponents ($F = 0.102, P > 0.05$). Aboveground biomass did not change with density. Significant differences existed between D1-D4 and D3-D4 for aboveground biomass, with other density pairs being non-significant.

#### 2.1.5 Effects of Population Density on Root Biomass Allocation and Allometric Relationships with Other Organs

Root biomass allocation varies among species with density. Root biomass in *C. macrocarpum* decreased significantly with density, showing a highly significant negative correlation ($F = 53.780, P < 0.001$). No significant differences existed among D1-D4. With increasing density, root biomass allocation showed a significant increasing trend, with highly significant positive correlation with density. D1 had significantly lower root biomass allocation than D2-D4, with significant differences among density treatments. Density had no significant effect on root:shoot allometric relationships ($F = 14.023, P = 0.321$) but had highly significant effects on individual size. Density significantly affected allometric relationships between root and stem biomass ($F = 0.028, P < 0.05$) but had no significant effect on allometric exponents ($F = 0.451, P > 0.05$). Root and stem biomass increased significantly with density ($F = 0.256, P < 0.001$), showing highly significant positive correlations, while root biomass did not change with density. No significant differences existed among D2-D3 and D2-D4, but significant differences occurred among other density pairs.

## 3. Discussion

### 3.1 Morphological Characteristics Analysis of *C. macrocarpum*

Higher plants establish aboveground architecture by regulating apical and lateral meristem activities, which are controlled by environmental signals, developmental stages, and genetic factors. This integrated regulation provides developmental plasticity and environmental adaptability. Previous studies show that with increasing density, plants maintain optimal height to maximize light capture, with smaller individuals reaching this optimum earlier. Our study found that as population density increased, *C. macrocarpum* exhibited different architectural systems: branch number and length decreased significantly. At D1, plants had more tertiary branches (maximum: 13 branches, total branch length up to 4330 cm), while at D4, most plants had only primary branches (maximum: 5 branches, total length only 536 cm). These changes, likely regulated by multiple genes, indicate that density significantly affected architecture construction by influencing stem apical meristem activity, thereby regulating the number and morphology of lateral organs.

### 3.2 Organ Biomass Allocation Pattern Analysis in *C. macrocarpum*

Ontogenetic effects on biomass allocation vary among species and reflect functional trade-offs during development, generally considered genetically determined. However, environmental conditions significantly affect allocation. *C. macrocarpum* adopts different optimal allocation strategies under varying competition intensities, showing plasticity in organ biomass allocation. With increasing density, all organ biomasses decreased, with D1 significantly higher than D2–D4. The magnitude of change followed: reproductive organs > stems > leaves > roots. Allocation patterns also changed: root and leaf allocation increased while stem, reproductive organ, and aboveground allocation decreased, consistent with optimal allocation theory under water, nutrient, and light limitation. This trade-off in resource allocation between above- and belowground parts reflects competition for resources. Increased root biomass enhances water and nutrient uptake, while increased leaf allocation (likely through leaf elongation) represents a shade-avoidance response mediated by phytochrome sensing of red:far-red light ratios.

### 3.3 Allometric Analysis of Organ Biomass Relationships in *C. macrocarpum*

With increasing density, height-organ biomass relationships showed simple allometry without complex linear patterns, though density significantly affected both allometric exponents and individual size. Height decreased significantly while organ biomasses traded off allocation to complete the life history. The allometric relationship between reproductive organs and root biomass did not change with density, representing apparent plasticity (size-dependent rather than density-responsive). In contrast, relationships between reproductive organs and aboveground biomass, and between leaves and other organs, showed true plasticity (significantly affected by density). Allometric exponents for leaf-stem and stem-aboveground biomass did not differ significantly from 3/4, consistent with metabolic scaling theory and representing apparent plasticity. The significant effects of density on leaf-other organ and reproductive-other organ allometric relationships indicate true plasticity, enabling *C. macrocarpum* to adapt to density changes and ensure life history completion.

## 4. Conclusion

Across all densities, *C. macrocarpum* showed allometric relationships between height and organ biomass. Branch number and length decreased significantly from D1 to D4 (from max 13 branches and 4330 cm length to max 5 branches and 536 cm length). Although total organ biomass decreased with density, root and leaf biomass allocation increased while reproductive and aboveground allocation decreased, consistent with optimal allocation theory under resource limitation. Allometric relationships between height and root biomass represented apparent plasticity, while those involving leaves and reproductive organs with other organs represented true plasticity. These changes enabled *C. macrocarpum* to develop different architectural systems and trade off resource allocation among organs to complete its life history.

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