Leaf Phenotypic Plasticity of Distylium chinense in Different Habitats of the Three Gorges Reservoir Area and Its Relationship with Soil Environmental Factors: Postprint

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Abstract

Investigating the ecological adaptability—phenotypic plasticity—of Distylium chinense under hydrological regimes of different habitats, along with its soil environmental influencing factors, holds significant ecological importance for its survival adaptation strategies in heterogeneous habitats. This study examined the plasticity of main leaf structural traits—leaf length (LL), leaf width (LW), leaf area (LA), leaf dry weight (LDW), and specific leaf area (SLA)—and their soil environmental influencing factors in 36 different populations of Distylium chinense across three heterogeneous habitats: natural water-level fluctuation zones, anti-season water-level fluctuation zones, and zones without water-level fluctuation rhythms. Differences in leaf traits of Distylium chinense across heterogeneous habitats were analyzed for significance, and the allometric growth relationships among LL, LW, LA, and LDW were described using classical allometric equations. Canonical correspondence analysis (CCA) was employed to investigate the relationships between leaf traits of Distylium chinense and soil environmental factors. The results showed that the five leaf functional traits of Distylium chinense populations—LL, LW, LA, LDW, and SLA—were all significantly different among heterogeneous habitats ($P < 0.05$), with mean coefficients of variation ranging from 4.80% to 26.12%, among which LA and SLA exhibited the highest coefficients of variation across all habitats. Across all heterogeneous habitats, Distylium chinense exhibited significant power-function allometric relationships between LW and LL, between LDW and LL, between LDW and LW, and between LDW and LA. Their allometric coefficients lg all showed highly significant differences ($P < 0.01$), while their allometric exponents exhibited consistent patterns: < 1 for LW vs. LL, > 1 for LDW vs. LL and LW, and 1 for LDW vs. LA, indicating that under different habitats, the growth rates of various leaf traits all followed the pattern: LA LDW > LL > LW. The substantial phenotypic plasticity of leaves and consistent allometric growth patterns across heterogeneous habitats indicate that Distylium chinense possesses a wide ecological amplitude when facing different hydrological regimes and demonstrates consistent growth patterns. CCA ordination results revealed that total phosphorus (TP), hydrolyzable nitrogen (AN), available potassium (AK), and soil water content (SWC) are the main influencing factors of leaf phenotypic plasticity in Distylium chinense. Distylium chinense primarily adjusts its leaf structural traits driven by these soil environmental factors, enabling it to exhibit optimal fitness in heterogeneous habitats with different hydrological regimes.

Full Text

Preamble

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Phenotypic Plasticity of *Distylium chinense* Leaves in Relation to Soil Environmental Factors in Heterogeneous Habitats in the Three Gorges Reservoir Region

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Abstract

Phenotypic plasticity is of great ecological significance for plant survival in heterogeneous habitats. With phenotypic plasticity, plants can maximize resource acquisition and effectively utilize resources in heterogeneous environments. This study investigated the phenotypic plasticity of leaf traits and their relationship with soil environmental factors in 36 *Distylium chinense* communities across three heterogeneous habitats (natural riparian zone, anti-seasonal water level fluctuation zone, and no water level fluctuation zone) in the Three Gorges Reservoir Region. The main structural leaf traits measured were leaf length (LL), leaf width (LW), leaf area (LA), leaf dry weight (LDW), and specific leaf area (SLA). Significance analysis was used to examine differences in leaf traits across heterogeneous habitats, and allometric relationships were described using classical allometric equations. Canonical Correspondence Analysis (CCA) was employed to explore relationships between leaf traits and soil environmental factors.

The results showed that: (1) All five functional traits (LL, LW, LA, LDW, and SLA) differed significantly ($P < 0.05$) among heterogeneous habitats, with mean coefficients of variation ranging from 4.80% to 26.12%. (2) Significant allometric relationships of power functions were observed between LW and LL, LDW and LL, LDW and LW, and LDW and LA across heterogeneous habitats. Allometric coefficients ( ) among 36 communities showed highly significant differences ($P < 0.01$), while allometric indices ( ) followed consistent patterns: LL and LW < 1, LDW and LL, LW > 1, and LDW and LA 1. Thus, the growth rate of leaf traits was: LA LDW > LL > LW. (3) CCA results indicated that total phosphorus (TP), total nitrogen (AN), available potassium (AK), and soil water content (SWC) were the main factors affecting leaf phenotypic plasticity. These soil environmental factors drive changes in leaf structural traits, enabling *D. chinense* to adapt to heterogeneous habitats with different hydrological regimes.

The high phenotypic plasticity and consistent allometric growth patterns of *D. chinense* leaves in heterogeneous habitats demonstrate wide ecological amplitude under different hydrological regimes. Additionally, soils in the Three Gorges Reservoir Region are deficient in N and K. Adding N and K during vegetation restoration could balance soil nutrition and promote *D. chinense* growth.

Keywords: *Distylium chinense*; phenotypic plasticity; Canonical Correspondence Analysis (CCA); heterogeneous habitats; allometry; environmental factors

Introduction

The relationship between plant traits and environmental response reflects the trade-offs between internal and external functions during plant adaptation, representing an important manifestation of plant survival strategies in specific environments. Phenotypic plasticity—the capacity of a single genotype to produce different phenotypes in response to environmental conditions—has attracted widespread attention from researchers in recent years. As a primary mechanism for organisms to adapt to environments without genetic variation, phenotypic plasticity enables plants to maximize resource acquisition, reallocate resources, and enhance fitness in variable environments, making it a crucial ecological strategy for adaptation to heterogeneous habitats.

While phenotypic plasticity is ubiquitous in plants, not all plasticity is adaptive. Adaptive plasticity refers to plastic responses that enhance organismal function and increase fitness in specific environments. Phenotypic plasticity can enhance species' resistance to adverse habitats, facilitate adaptation to heterogeneous environments, and provide the phenotypic basis for biological adaptation, resulting in broader ecological amplitudes. Plant adaptability to heterogeneous habitats can be measured by the degree of phenotypic plasticity, which, along with genetic differentiation (including ecological differentiation), represents two primary mechanisms for biological adaptation to heterogeneous environments. In phenotypic plasticity, genotype and phenotype are no longer simply correlated, as phenotype is determined not only by genotype but also by environmental factors during development.

Plant leaves are the primary organs for gas exchange and energy conversion in ecosystems. Leaf traits represent specific manifestations of basic behaviors and functions formed in response to environmental changes, 主要包括 structural and functional traits, which together reflect plants' survival adaptation strategies for maximizing carbon gain. Phenotypic plasticity of leaf traits has important ecological and evolutionary significance for plant population survival strategies in heterogeneous habitats.

Flooding is a critical form of aquatic environmental stress that affects plant metabolism, physiology, and morphology. Previous studies found that after complete submergence for 120 days, *Salix variegata* survival rates remained high, while *Hemarthria altissima* and *Cynodon dactylon* could tolerate submergence for up to 180 days. Research has shown that flood-tolerant species often adapt to environmental fluctuations through high phenotypic plasticity to survive flooding periods. For example, *Alnus japonica* adapts to flooding by increasing stem thickness and developing adventitious roots to alleviate oxygen deficiency, while *Oenanthe javanica* produces submerged leaves with distinct anatomical structures from aerial leaves to better adapt to flooded environments.

Phenotypic plasticity is influenced by both biotic and abiotic factors, including light, nutrients, water, and temperature. Under global climate change, whether plant phenotypic plasticity can adapt to these changes and how these changes affect plasticity are important concerns. Most phenotypic plasticity research has involved controlled gradient experiments simulating single factors (e.g., light or dissolved oxygen), lacking large-scale studies in natural environments. Population-level studies of phenotypic plasticity in natural environments can reveal plants' responses and ecological adaptation significance, enriching understanding of plant population distribution.

Distylium chinense (Hamamelidaceae) is a perennial evergreen shrub in riparian zones of the Three Gorges Reservoir Region, serving as an excellent species for soil consolidation and bank protection. It can grow in various heterogeneous habitats, including terrestrial and wet environments, and has strong flooding tolerance. With high ornamental value, it is also a superior bonsai species. However, with the construction of hydropower projects and human overexploitation, natural habitats have been submerged, leading to reduced wild resources and genetic diversity. Wild *D. chinense* communities are now only sporadically distributed in valleys and streams along the Wu River and Yangtze River. Previous research using ISSR molecular markers showed that *D. chinense* populations have rich genetic diversity but low genetic differentiation among populations, suggesting high phenotypic plasticity.

This study investigated leaf trait phenotypic plasticity of *D. chinense* populations in three heterogeneous habitats (natural riparian zone, anti-seasonal water level fluctuation zone, and no water level fluctuation zone) and used CCA to explore relationships with soil environmental factors. We addressed two questions: (1) Can phenotypic plasticity reveal the ecological adaptability of *D. chinense* in heterogeneous habitats with different hydrological regimes? (2) Which soil environmental factors are the main drivers of leaf phenotypic plasticity?

1. Study Area Overview

The study area included the Xiangxi River in the Three Gorges Reservoir Region, belonging to the subtropical humid monsoon climate zone with mild, humid conditions and abundant heat and water resources suitable for most thermophilic plants. *Distylium chinense* populations grow in riparian zones of the Three Gorges area, experiencing water level fluctuations during flood seasons or reservoir impoundment. The flora is dominated by cosmopolitan, pantropical, and north temperate species, with life forms mainly dwarf phanerophytes and annual plants. Main associated species include *Ficus tikoua*, *Geum aleppicum*, *Equisetum ramosissimum*, *Cornus quinquenervis*, and *Imperata cylindrica*. The Three Gorges Reservoir drawdown zone contains 237 vascular plant species, including Chinese endemics that provide rich resources for vegetation restoration. *Distylium chinense* is a dominant shrub species widely distributed along the Yangtze River and its tributaries.

1.1 Sampling

Thirty-six *D. chinense* sampling sites were established across three heterogeneous habitats with different hydrological regimes:

1. **Natural riparian zone (NRZ)**: Four natural sites (A1-A4, A5-A8, A9-A12, A13-A16) including Zhuzixi, Bailong Guojiang, and Gulongxi in Yichang. These areas are affected by summer flood season submergence (maximum depth 170-175 m, duration up to 237 days) but not by Three Gorges Reservoir water level regulation.
2. **Anti-seasonal water level fluctuation zone (ASWLFZ)**: Eight sites (B1-B4, B5-B8) in the Xiangxi River drawdown zone of Zigui County and Xingshan County. These areas were planted with one-year-old *D. chinense* for vegetation restoration and are affected by reservoir operation (winter impoundment, summer drainage).
3. **No water level fluctuation zone (NWLFZ)**: Eight sites (C1-C4, C5-C8, C9-C12) including the Three Gorges Botanical Garden and Wushan Rare Botanical Garden, unaffected by flood season or reservoir impoundment.

Basic information for each sampling site is shown in [Figure 1: see original paper] and .

2. Soil Environmental Factor Analysis and Experimental Methods

During sampling, undisturbed soil samples (0-20 cm layer) were collected from each quadrat using a cutting ring. Soil physicochemical properties were analyzed following standard methods. Measured indicators included: soil organic matter (OM), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), available potassium (AK), and soil water content (SWC).

- TN: Kjeldahl method
- TP: HClO -H SO digestion with molybdenum-antimony colorimetry
- TK: HF-HClO digestion with flame photometry
- AN: Alkali hydrolysis diffusion method
- AP: NaHCO extraction with molybdenum-antimony colorimetry
- AK: Ammonium acetate extraction with flame photometry
- SWC: MP-406 I soil moisture meter

Soil environmental factors across habitats are shown in .

3. Quantitative Trait Measurement Methods

In each 5 m × 5 m quadrat, five healthy, fully expanded leaves from upper branches (including all cardinal directions) were collected from each of 36 *D. chinense* populations across three habitats to avoid self-shading. Leaves were numbered and measured for:

- Leaf length (LL) and leaf width (LW) using millimeter rulers
- Leaf area (LA) using a LI-3000A leaf area meter
- Leaf dry weight (LDW) using an analytical balance after oven-drying
- Specific leaf area (SLA) calculated as SLA = LA / LDW

4. Statistical Analysis Methods

Data were analyzed using Microsoft Excel 2013 and SPSS 22.0. Variance analysis and correlation analysis were performed on leaf traits across heterogeneous habitats. Significance testing examined differences in leaf traits among habitats. Allometric relationships between traits were described using the classical allometric equation Y = X^ . Variables were log-transformed for linear regression, and analysis of covariance compared differences in allometric index ( ) and coefficient (, i.e., Y-intercept) among habitats.

Canonical Correspondence Analysis (CCA) was performed using CANOCO 5.0 software to analyze relationships between plant traits and soil environmental factors. Species trait matrices (LL, LW, LDW, LA, SLA) and environmental factor matrices were log-transformed to approach normal distribution. Monte Carlo significance tests were conducted to assess the significance of environmental factors' explanatory power on plant traits.

3. Results and Analysis

3.1 Soil Environmental Heterogeneity in Different Habitats

In the Three Gorges Reservoir Region, all environmental factors except altitude and TK showed highly significant differences ($P < 0.01$) among habitats, indicating heterogeneity of the same environmental factors across different habitats.

3.2 Leaf Quantitative Traits and Plasticity Analysis

Leaf traits of *D. chinense* differed significantly ($P < 0.05$) among habitats, indicating real differences among populations within each habitat and enabling plasticity analysis. Plasticity within the same habitat was reflected by maximum values, standard deviations, and coefficients of variation (CV). The mean CV across habitats ranged from 4.80% to 26.12%, with an average of 14.70%, indicating high plasticity. Natural riparian zones (A1-A4, A5-A8) showed the highest mean CV (18.93%), suggesting that high plasticity is an important mechanism for adapting to heterogeneous habitats.

shows quantitative leaf traits and coefficients of variation across heterogeneous habitats.

3.3 Allometric Growth Patterns of Leaf Traits

Leaf growth involves increases in length and width, accompanied by leaf dry weight accumulation. Leaf area reflects photosynthetic capacity, while leaf dry weight reflects construction cost. Statistical analysis revealed significant allometric relationships (power functions) between LW and LL, LDW and LL, LDW and LW, and LDW and LA across all heterogeneous habitats.

The allometric index ( ) values for LL and LDW were all < 1, while those for LDW and LL, LW were > 1, and LDW and LA were 1. This indicates that during leaf growth, LDW grows faster than LL and LW, while LA growth rate is similar to LDW. The growth rate of leaf traits followed a consistent pattern across habitats: LA LDW > LL > LW.

3.4 Plasticity Analysis of Allometric Parameters

Allometric parameters consist of coefficient ( ) and index ( ). Analysis of covariance showed that both and differed highly significantly ($P < 0.01$) among heterogeneous habitats, indicating large plasticity in allometric relationships. While allometric indices remained stable within habitats, the coefficients showed large variation, suggesting high plasticity in the starting points of allometric growth and sensitivity of trait relationships to environmental changes.

presents allometric equation parameters for leaf traits across habitats.

3.5 Relationships Between Leaf Traits and Environmental Factors

CCA was used to analyze correlations between leaf traits and environmental factors. The first two axes explained 76.65% and 91.66% of trait variation, respectively. Monte Carlo tests showed all canonical axes were highly significantly correlated with leaf traits ($P < 0.01$), confirming reliable ordination results.

The first axis was primarily influenced by TP, AN, TK, and TN, while the second axis was mainly affected by AK, SWC, OM, and AP. Correlation coefficients were -0.8555, 0.7983, -0.6805, and -0.6078, respectively. The main factors affecting leaf structural traits (SLA, LA, LL, LW) were TP, AN, AK, and SWC, with correlation coefficients of -0.7580, -0.7479, -0.6092, and -0.6051.

Sampling sites were distributed sequentially from bottom to top along the second axis: C1-C4, C5-C8 (no water fluctuation zone), C9-C12; B1-B4, B5-B8 (anti-seasonal reservoir drawdown zone); and A1-A4, A5-A8, A9-A12, A13-A16 (natural riparian zone). Thus, TP, AN, AK, and SWC are the main factors influencing *D. chinense* population distribution and leaf phenotypic plasticity.

[Figure 2: see original paper] shows the CCA ordination diagram of leaf traits and environmental factors.

4. Discussion

4.1 Leaf Phenotypic Plasticity and Population Ecological Adaptation

Phenotypic plasticity plays a crucial role in plant adaptation to heterogeneous environments, serving as an important ecological strategy. Plants with high plasticity can alter morphology to better adapt, increasing fitness. Such plasticity responses that enhance fitness are termed adaptive plasticity.

ISSR molecular marker studies have shown that *D. chinense* has rich genetic diversity but low genetic differentiation among populations (10.8% of total variation), with 89.2% within-population variation. This indicates that phenotypic plasticity within populations is the main adaptation mechanism. In this study, significant differences in LL, LW, LA, and LDW among habitats ($P < 0.05$) demonstrated strong plasticity in leaf traits, while consistent allometric patterns across habitats showed stable growth strategies.

The coefficient , representing the Y-intercept in allometric relationships, reflects environmental sensitivity. Significant differences in among habitats indicate high plasticity in the starting points of allometric growth. The consistent pattern LA LDW > LL > LW suggests that despite high plasticity, *D. chinense* maintains orderly growth across heterogeneous habitats, representing an adaptation mechanism.

The coefficient of variation (4.80%-26.12%) reflects relative trait variation and plasticity. The highest CV for leaf width occurred in the Xiangxi River drawdown zone (B1-B4), which experiences the longest flooding duration (170-175 m, up to 237 days) and extreme drought during dry periods, creating the harshest habitat with high seasonal variation in nutrients, light, and competition.

Specific leaf area (SLA) is a key indicator of photosynthetic capacity and resource acquisition strategy. Lower SLA values in the harshest habitats (B1-B4, B5-B8) suggest that leaves allocate more dry mass to protective structures, increasing leaf thickness or mesophyll density to maintain water balance and reduce respiratory carbon loss, thereby maintaining positive carbon balance through extended leaf lifespan.

4.2 Main Environmental Factors Affecting Growth and Leaf Plasticity

Plant resources and environmental conditions exhibit heterogeneity even at small scales. Nutrient heterogeneity acts as selective pressure, driving ecological adaptation strategies. N, P, K, water, and metal ions are primary growth factors. Potassium regulates stomata, activates key photosynthetic enzymes (Rubisco), and participates in assimilate transport, enhancing plant resistance.

During flooding, *D. chinense* stomata remain closed, limiting photosynthesis. High AK content may rapidly activate photosynthetic enzymes after flooding, enabling quick recovery. Research indicates optimal available K concentration for vegetation is 200 mg/kg, below which species diversity increases with K concentration. The studied habitats had average AK concentrations of (94.78±4.47) mg/kg, all below 200 mg/kg, indicating K limitation. Additionally, N deficiency and low N:P ratios (<20) suggest N and K limitations across all habitats.

CCA results confirmed that TP, AN, AK, and SWC are the main factors affecting leaf phenotypic plasticity and population distribution. Different habitats require different adaptation strategies, with soil environmental factors driving plasticity responses.

4.3 Recommendations for *D. chinense* Restoration in Three Gorges Reservoir Drawdown Zone

Distylium chinense has compact form and dense foliage that prevents soil water loss, making it excellent for soil consolidation and bank protection. It plays an important role in drawdown zone ecosystem restoration. Although naturally flood-tolerant and adaptable to various habitats, hydropower development and human impacts threaten its survival.

Based on our results, soils in the region are N- and K-deficient. Appropriate N and K addition during vegetation restoration could balance soil nutrition and improve habitat conditions. Further research is needed to determine optimal ratios of these nutrients for *D. chinense* growth.

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