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Environmental Gradients Drive Leaf Morphological Diversity in the Mangrove *Avicennia marina* across Coastal Wetlands of the Indian West Coast

Thasny KK
Cochin University of Science and Technology
Bhavadas N
Cochin University of Science and Technology
Sreekanth PM
sreekanthpm@cusat.ac.in

Cochin University of Science and Technology

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Abstract

Understanding how mangroves respond to environmental gradients is essential for predicting their resilience under changing climatic conditions. This study examined spatial variation in leaf morphology of *Avicennia marina* across five populations (n = 178) along the west coast of India (Gujarat, Mumbai, Goa, Karnataka, and Kerala) and evaluated its relationship with hydroclimatic variables. Leaf morphological traits, including leaf length, breadth, petiole length, leaf area, perimeter, tip angle, base angle, and shape index, were measured and analysed in relation to temperature, precipitation, relative humidity, salinity, and tidal amplitude. Significant differences in leaf morphology were observed among populations. Kerala and Goa populations exhibited larger leaf dimensions, whereas Gujarat populations were characterized by smaller and narrower leaves. Correlation analyses revealed positive relationships between leaf area and temperature ($R^2 = 0.72$), humidity ($R^2 = 0.81$), and precipitation ($R^2 = 0.85$), while negative associations were observed with salinity and tidal amplitude. Shape index was strongly negatively correlated with salinity ($R^2 = 0.92$) and tidal amplitude ($R^2 = 0.88$). Principal component analysis explained 57.0% of the total morphological variation and showed clear differentiation among populations, particularly between Gujarat and Kerala. The patterns observed in this study indicate that hydrological and hydroclimatic factors are significant drivers of leaf trait variation in *A. marina*, demonstrating the species' ability to respond to contrasting estuarine environments. These findings support that environmental heterogeneity across coastal wetlands shapes leaf morphological variation through the joined influence of local adaptation and phenotypic plasticity. By improving our understanding of adaptive responses in mangrove ecosystems, this study provides an ecological basis for conserving geographically distinct populations and informs Biodiversity conservation, climate-resilient wetland restoration and adaptive coastal wetland management

Introduction

Mangrove forests are among the most productive and ecologically important coastal wetlands, providing essential ecosystem services including shoreline stabilization, carbon sequestration, nutrient cycling, and habitat support for diverse flora and fauna (Alongi 2020). Despite their ecological and socioeconomic importance, mangrove ecosystems are increasingly threatened by climate change, sea-level rise, salinity intrusion, altered hydrological regimes, and anthropogenic disturbances (Alongi 2023). Recent studies have highlighted hydroclimatic variability as a key driver of mangrove ecosystem structure, functioning, and resilience, influencing species distribution, productivity, and adaptive responses to environmental stress (Ferreira et al. 2024; Deb Burman and Das 2024).

Avicennia marina (Forssk.) Vierh. is the most widely distributed mangrove species in the Indo-West Pacific region and is a dominant component of mangrove communities along the Indian coastline. Along the west coast of India, the species occurs across a broad environmental gradient extending from the arid and hypersaline coastal habitats of Gujarat to the humid estuarine ecosystems of Goa and Kerala. These regions differ markedly in salinity, precipitation, temperature, tidal amplitude, sediment characteristics, and freshwater availability, providing a natural framework for investigating patterns of

phenotypic variation in relation to environmental heterogeneity (Kathiresan and Bingham 2001; Martínez-Díaz and Reef 2023).

Plant functional traits are widely recognized as indicators of species responses to environmental change. Among these, leaf morphological traits are particularly important because they directly influence photosynthesis, transpiration, carbon gain, water-use efficiency, and tolerance to abiotic stress. Variations in leaf size and shape reflect trade-offs between resource acquisition and water conservation and can therefore provide valuable insights into plant performance across environmental gradients. In mangroves, alterations in leaf structure and composition under saline and hydrologically stressful conditions demonstrate their sensitivity to environmental change and their potential utility as indicators of ecosystem condition (Dittmann et al. 2022). Consequently, trait-based approaches have become increasingly important for understanding ecosystem resilience and predicting plant responses to climatic variability (Adams et al. 2023; Dookie et al. 2023).

Leaves of A. marina possess several structural adaptations that facilitate survival in saline and periodically inundated environments, including succulent tissues, thick cuticles, hypodermal layers, and specialized salt-secreting glands (Naidoo 1985; Reef and Lovelock 2014). These adaptations contribute to osmotic regulation, salt tolerance, and water conservation. Environmental stressors such as elevated salinity, drought, and prolonged inundation can influence leaf morphology by reducing leaf area and modifying leaf shape, thereby improving water-use efficiency and minimizing physiological stress. Phenotypic plasticity enables such trait adjustments in response to environmental variation and is considered a key mechanism underpinning resilience in heterogeneous coastal environments. Recent studies suggest that populations exposed to greater environmental variability often exhibit enhanced adaptive capacity, improving their persistence under changing climatic conditions (Kennedy et al. 2022; Adams et al. 2023). Furthermore, molecular investigations indicate that stress tolerance in A. marina involves complex regulatory pathways associated with salinity adaptation and environmental stress responses (Feng et al. 2023; Li et al. 2023).

The west coast of India is currently undergoing rapid environmental change driven by urbanization, coastal development, altered hydrological regimes, and climate-induced shifts in precipitation and salinity patterns. Although A. marina is one of the dominant mangrove species in the region, studies examining leaf morphological variation across broad hydroclimatic gradients remain scarce. Previous investigations have primarily focused on local ecological assessments, physiological responses, or species distribution patterns, whereas comparative analyses linking leaf morphological variation to climatic and hydrological drivers across geographically distinct populations are limited. This knowledge gap constrains our understanding of how functional trait variation contributes to the ecological resilience of mangrove wetlands and their capacity to respond to ongoing environmental change.

Understanding trait–environment relationships is increasingly important for predicting mangrove responses to future climate scenarios and for informing conservation and restoration strategies. As sea-level rise, altered precipitation regimes, and increasing climatic extremes continue to modify salinity,

inundation patterns, and sediment dynamics, population-level variation in functional traits may play a critical role in determining ecosystem resilience and recovery (Dahdouh-Guebas et al. 2022; Saintilan et al. 2022). Consequently, evaluating leaf morphological variation across environmental gradients can provide valuable insights into mechanisms of phenotypic plasticity while generating information relevant to climate-resilient mangrove restoration, wetland conservation, and adaptive coastal ecosystem management.

Therefore, this study investigated spatial variation in leaf morphology of A. marina across five regions along the west coast of India—Gujarat, Mumbai, Goa, Karnataka, and Kerala—representing contrasting hydroclimatic conditions. Specifically, we aimed to: (i) quantify and compare leaf morphological traits among populations; (ii) examine relationships between leaf traits and environmental variables, including salinity, tidal amplitude, temperature, humidity, and precipitation; and (iii) evaluate the implications of trait–environment relationships for understanding mangrove responses to environmental change and supporting wetland management.

Materials and methods

Study site and sampling

Five natural populations of *Avicennia marina* located along the western coast of India were sampled for leaf morphometric analysis: Sachana (Gujarat), Niroli (Maharashtra), Chorao Island (Goa), Kundapura (Karnataka), and Puthuvype (Kerala). Geographic coordinates were recorded using a handheld GPS receiver. Sampling sites were selected to represent major hydroclimatic zones along the west coast of India, encompassing variations in salinity, rainfall, tidal amplitude, and temperature.

A total of 178 individual trees were sampled across the five populations. Species identification was confirmed by comparison with authenticated voucher specimens deposited at the Kerala Forest Research Institute (KFRI), Peechi, Kerala, India, and the Royal Botanic Gardens Kew Herbarium, United Kingdom. Reference voucher specimens included KFRI accession numbers 4123 and 4124 and Royal Botanic Gardens Kew Herbarium accession number K0008854644 for *Avicennia marina*. Additional reference material was examined under KFRI accession number 1759. These individuals encountered along pre-selected transects within each mangrove stand were assessed for inclusion. At each site, 35–40 healthy, mature trees were selected, maintaining a minimum distance of 10–15 m between sampled individuals to reduce the likelihood of sampling clonally related trees. From each selected tree, 35–40 fully expanded, healthy leaves were collected from the upper and middle canopy. Leaves showing signs of senescence, disease, herbivory, or mechanical damage were excluded from the analysis.

Table 1
Sampling locations, geographic coordinates, and environmental characteristics of five natural populations of *A. marina*.

Region / Site	Latitude (°N)	Longitude (°E)	Environmental Setting
Gujarat (Sachana)	23.08	72.17	Arid to semi-arid, hypersaline coasts with sparse mangrove stands.
Mumbai (Niroli, Mumbai)	19.04	73.02	Urban–estuarine interface with moderate salinity and tidal fluctuation.
Goa (Dr. Salim Ali NP)	15.50	73.83	Tropical monsoonal climate with moderate rainfall and tidal creeks.
Karnataka (Kunthapura)	13.63	74.69	Coastal wetlands influenced by seasonal river discharge and estuarine salinity shifts.
Kerala (Puthuvype)	9.97	76.26	Humid tropical environment with high rainfall and relatively stable estuarine salinity.

Leaf Morphometric Measurements

Leaf morphological traits were quantified using fully expanded, healthy leaves collected from each sampled tree. Leaf length (LL) was measured as the distance from the base of the lamina at the point of petiole insertion to the leaf apex, while leaf width (LW) was recorded as the maximum width perpendicular to the midrib. Petiole length (PL) was measured from the point of stem attachment to the base of the lamina.

Leaf area (LA) was determined by tracing individual leaves onto 1 mm² graph paper, followed by digital image acquisition and analysis using the software ImageJ v1.54 (National Institutes of Health, Bethesda, MD, USA). Images were calibrated using a known scale, and the enclosed leaf area was quantified automatically. To characterize leaf shape variation, the Leaf Shape Index (LSI) was calculated as the ratio of leaf length to leaf width (LL/LW).

Angular traits included leaf tip angle (LTA) and leaf base angle (LBA). The leaf tip angle was measured at the leaf apex following the method described by Montgomery (1911), whereas the leaf base angle was measured at the junction between the lamina and petiole. All measurements were recorded for each leaf and subsequently used for statistical analyses of morphological variation among populations of *A. marina*

Hydroclimatic Data Collection

Hydroclimatic variables were compiled for each sampling location to evaluate their potential influence on leaf morphological variation in *Avicennia marina*. The variables considered included mean annual temperature (°C), relative humidity (%), annual precipitation (mm yr^{-1}), salinity (ppt), and tidal amplitude (m). Climatic data were obtained from the India Meteorological Department (IMD, 2019), whereas salinity

and tidal amplitude data were compiled from regional coastal and mangrove datasets (Nayak and Bahuguna 2001; Raghavan et al. 2019).

These variables were selected because they represent major environmental drivers governing mangrove growth, physiological performance, water-use efficiency, and phenotypic adaptation across coastal habitats. Variations in salinity, temperature, humidity, precipitation, and tidal inundation have been shown to influence leaf functional traits and morphological responses in mangrove species, including *A. marina* (Ahmed et al. 2022; Ball and Adams 2022; Nizam et al. 2022).

Association Between Leaf Traits and Hydroclimatic Gradients

The relationship between leaf morphological variation and environmental conditions was investigated across five populations of *Avicennia marina* distributed along the western coast of India. Mean values of leaf length (LL), leaf width (LW), petiole length (PL), leaf area (LA), leaf shape index (LSI), leaf tip angle (LTA), and leaf base angle (LBA) were examined in relation to hydroclimatic variables, including mean annual temperature, relative humidity, annual precipitation, salinity, and tidal amplitude.

Hydroclimatic variables were selected because they represent major ecological drivers influencing mangrove growth, water relations, salinity tolerance, and phenotypic plasticity. Comparative and multivariate approaches were employed to evaluate patterns of morphological variation among populations and to identify associations between leaf traits and environmental gradients. These analyses were used to assess the extent to which geographic and hydroclimatic heterogeneity contributes to morphological differentiation in *A. marina* populations.

Statistical Analysis

Descriptive statistics were calculated for all leaf morphological traits. Population-level variation in leaf morphology was visualized using comparative boxplots to examine differences among the five coastal populations.

Relationships among hydroclimatic variables were examined using Pearson's correlation analysis and visualized through correlation heatmaps. Associations between leaf morphological traits and hydroclimatic variables were further evaluated using Pearson's correlation coefficients to identify environmental factors influencing trait variation.

Principal Component Analysis (PCA) was performed on standardized leaf morphological traits to identify the major axes of variation and determine the contribution of individual traits to population differentiation. Hierarchical Cluster Analysis (HCA) based on Euclidean distance and Ward's linkage method was conducted to assess similarities among populations and to visualize clustering patterns based on leaf morphological characteristics.

Prior to multivariate analyses, all variables were standardized to eliminate the effects of differing measurement scales. All statistical analyses and graphical visualizations were performed in R version

4.4.1 (R Core Team, 2024), and statistical significance was evaluated at $P < 0.05$.

Result

Variation in Leaf Morphological Traits Among Populations

Representative leaves collected from each population exhibited clear differences in size and shape. Collected 179 samples from 5 populations. Gujarat leaves were notably smaller and narrower, whereas Kerala and Goa leaves were larger and broader (Fig. 1). Mumbai and Karnataka leaves displayed in-between dimensions, with elongated lamina in Mumbai contrasting with moderately broad leaves in Karnataka. These visual differences were reliable with the morphometric patterns quantified through ANOVA and multivariate analysis (Table 2).

Variation in leaf morphology of *A. marina* across populations

Leaf length varied from 11.8cm(Goa),8.5cm(Puthuvype/Kerala),8.2cm Mumbai(Bombay),6.4 cm (Gujarat)and 6.6 cm Karnataka with differences in lamina breadth and shape reflecting adaptations to local hydroclimatic conditions

Table 2
Mean (± SE) values of leaf morphological traits of *A. marina* populations

Site	Leaf Length (LL, cm)	Leaf Width (LW, cm)	Petiole Length (PL, cm)	Leaf Area (LA, cm²)	Leaf Shape Index (LSI)
Gujarat	4.91 ± 0.08	1.96 ± 0.05	0.80 ± 0.04	9.65 ± 0.31	2.55 ± 0.08
Mumbai	6.99 ± 0.12	2.96 ± 0.07	1.06 ± 0.03	20.68 ± 0.60	2.40 ± 0.07
Goa	9.05 ± 0.15	5.02 ± 0.09	1.17 ± 0.04	45.42 ± 1.09	1.82 ± 0.05
Karnataka	8.08 ± 0.12	3.61 ± 0.06	1.06 ± 0.02	29.25 ± 0.75	2.25 ± 0.04
Kerala	10.21 ± 0.16	5.51 ± 0.09	1.29 ± 0.04	56.31 ± 1.31	1.86 ± 0.04

Gujarat populations exhibited the smallest leaf size but highest LSI, while Kerala and Goa populations displayed larger lamina with lower LSI. Mumbai and Karnataka showed intermediate morphologies.

Significant variation in leaf morphological traits was observed among the five west coast populations of *Avicennia marina* (Bombay, Goa, Gujarat, Karnataka, and Kerala) (Fig. 2). Leaf length and petiole length were highest in the Kerala and Bombay populations, whereas the Gujarat population recorded the lowest values for most traits. Leaf breadth varied among populations, with Goa exhibiting the greatest mean value. The leaf length-to-breadth ratio (LB_Ratio) was higher in Karnataka and Kerala, indicating relatively more elongated leaves in these populations. Tip angle and base angle also differed across populations, with Kerala and Goa showing higher mean values than Gujarat. In contrast, leaf perimeter exhibited comparatively limited variation among populations. Overall, the Kerala and Bombay populations were

characterized by larger leaf dimensions, whereas the Gujarat population generally displayed smaller leaf morphological attributes.

Boxplots showing variation in leaf morphological traits of *A. marina* across five study sites

Traits include (a) Leaf Length (LL), (b) Leaf Width (LW), (c) Petiole Length (PL), (d) Leaf Area (LA), and (e) Leaf Shape Index (LSI). Boxes represent the interquartile range, the horizontal line indicates the median, whiskers denote 1.5 × IQR, and circles represent outliers. Gujarat populations show significantly smaller, narrower leaves, while Kerala and Goa populations display larger, broader leaves. Bombay and Karnataka exhibit intermediate traits.

Hydroclimatic Data Collection

Variables include annual mean air temperature, mean relative humidity, annual precipitation, estimated surface-water salinity, and typical tidal amplitude. These data illustrate the pronounced north–south hydroclimatic gradient—from the arid, high-salinity coasts of Gujarat to the humid, low-salinity environments of Kerala—providing essential context for interpreting geographic variation in *A. marina* leaf morphology (Table 3)

Table 3
Climatic and hydrographic parameters for five representative mangrove sampling sites along India's west coast.

Site (representative station)	Mean temp (°C)	Mean rel. humidity (%)	Annual precip. (mm yr^{-1})	Salinity (ppt)	Tidal amp. (m)
Gujarat (Sachana, Saurashtra/Kutch coast)	27.5	55–65	600–900	30–36	2.5–4.0
Mumbai (Niroli	25.8	70–78	2000–2600	24–30	2.0–3.0.
Goa (Chorao Island)	26.5	75–82	2500–3200	18–28	1.5–2.5.
Karnataka (Kunthapura / coastal Karnataka)	26.7	70–78	1800–2800	15–25	1.5–2.5.
Kerala (Puthuvype / Kochi coast)	27.0	78–86	2500–3500	10–20	1.0–2.0.

Statistical Analysis

Relationships among Hydroclimatic Variables

Correlation analysis revealed distinct associations among hydroclimatic variables across the five study sites (Fig. 3). Relative humidity was strongly positively correlated with precipitation and negatively correlated with salinity. Salinity exhibited negative correlations with both precipitation and humidity,

whereas tidal amplitude showed comparatively weaker correlations with the other hydroclimatic variables.

Leaf morphological traits were also significantly associated with environmental variables. Leaf area showed positive correlations with mean temperature ($R^2 = 0.72$), relative humidity ($R^2 = 0.81$), and precipitation ($R^2 = 0.85$). In contrast, shape index was negatively correlated with salinity ($R^2 = 0.92$) and tidal amplitude ($R^2 = 0.88$). These results indicate clear associations between hydroclimatic conditions and leaf morphological variation among *Avicennia marina* populations along the west coast of India.

Relationships between hydroclimatic variables and leaf morphological traits in *Avicennia marina*. Leaf area showed positive correlations with mean temperature ($R^2 = 0.72$), relative humidity ($R^2 = 0.81$), and precipitation ($R^2 = 0.85$), whereas shape index was negatively correlated with salinity ($R^2 = 0.92$) and tidal amplitude ($R^2 = 0.88$). Dashed lines indicate linear regression fits.

The heatmap revealed clear associations between leaf traits and hydroclimatic variables (Fig. 4). Leaf area was positively correlated with temperature, humidity, and precipitation, and negatively correlated with salinity and tidal amplitude. Similarly, shape index showed positive correlations with humidity and precipitation, but negative correlations with salinity and tidal amplitude.

Correlation analysis showed a strong positive relationship between relative humidity and precipitation ($r = 1.00$). Both variables were strongly negatively correlated with salinity ($r = -0.88$ and -0.86, respectively) and tidal amplitude ($r = -0.95$ and -0.93, respectively). Salinity and tidal amplitude exhibited a strong positive correlation ($r = 0.98$), while temperature showed relatively weak correlations with the other climatic variables (Fig. 4).

Principal Component Analysis

Principal Component Analysis (PCA) of leaf morphometric traits revealed clear regional differentiation among populations across the five coastal states. The first two principal components (PC1 and PC2) together explained 57.0% of the total variance, with PC1 (31.4%) and PC2 (25.6%) representing major axes of morphological variation (Fig. 5)

PC1 exhibited strong positive loadings for leaf length, leaf breadth, and petiole length, thereby representing overall leaf size. Populations from Kerala and Bombay were positioned on the positive side of PC1, indicating larger, broader leaves typical of humid coastal environments. In contrast, Gujarat populations clustered on the negative axis of PC1, characterized by narrower and smaller leaves, a pattern consistent with adaptation to arid and saline habitats.PC2 was primarily influenced by base angle, tip angle, and the length-to-breadth (L/B) ratio, reflecting variation in leaf shape. Goa and Karnataka populations occupied intermediate positions, indicating transitional morphologies along the west coast gradient.

Although the confidence ellipses for the five regions partially overlapped, distinct clustering trends were evident, suggesting that leaf morphology is environmentally structured rather than entirely plastic. The

orientation of trait vectors showed that petiole length and leaf breadth contributed strongly to PC1, while L/B ratio and tip angle were dominant along PC2. These results indicate that leaf size and shape jointly respond to climatic and hydrological gradients from arid (Gujarat) to humid (Kerala) zones, reflecting adaptive divergence across the species' geographic range.

Cluster Analysis

Hierarchical cluster analysis of leaf morphological traits revealed three major clusters corresponding to geographic regions along the west coast of India (Fig. 6). Cluster 1 (Gujarat) formed a distinct branch, clearly separated from the rest of the populations, with Gujarat samples clustering firmly together and exhibiting smaller, narrower leaves adapted dry and hypersaline conditions. Cluster 2 (Goa + Karnataka) gathered populations from Goa and Karnataka into a transitional cluster, indicating similarity in leaf morphology traits likely influenced by shared hydroclimatic conditions and transitional environments between the arid north and humid south. Cluster 3 (Mumbai + Kerala) combined populations from Mumbai and Kerala, categorized by broader, larger leaves typical of high rainfall and humid estuarine environments in southern and central coastal regions. This clear clustering pattern highlights the role of regional hydroclimatic gradients in determining morphological divergence in *Avicennia marina*, corroborating the PCA results and supporting the population-level structuring of traits along the environmental gradient

Hierarchical clustering dendrogram of Avicennia marina populations based on leaf morphological traits.Three distinct clusters were observed: Cluster 1 (Gujarat), Cluster 2 (Goa + Karnataka), and Cluster 3 (Mumbai + Kerala). Red vertical lines represent the major cluster divisions.

Discussion

Spatial variation in leaf morphology across hydroclimatic gradients

This study revealed substantial variation in leaf morphological traits of *Avicennia marina* across the hydroclimatic gradient of the Indian west coast. Populations occupying environmentally contrasting regions exhibited distinct leaf characteristics: Gujarat populations produced smaller, narrower leaves, while Kerala and Goa populations produced larger leaves. These findings suggest that leaf morphology in *A. marina* is strongly influenced by environmental conditions and is consistent with patterns reported across the species' global distribution range, where climatic and hydrological factors contribute significantly to trait variation (Martínez-Díaz and Reef, 2023).

The marked differentiation between mangrove populations in Gujarat and Kerala reflects the exceptional environmental heterogeneity of the Indian west coast. Gujarat mangroves experience hypersaline conditions, low freshwater input, and high evaporative demand, whereas Kerala populations occur in humid estuarine systems characterized by abundant rainfall and relatively stable salinity regimes. Such contrasting environmental conditions likely contribute to the pronounced morphological divergence observed among populations.

The reduction in leaf size observed in Gujarat is likely associated with the hypersaline and water-limited conditions characteristic of arid coastal environments. Under elevated salinity, mangroves experience reduced water availability due to osmotic constraints, resulting in physiological adjustments that favor water conservation (Naidoo, 1985; Ahmed et al., 2022). Smaller leaves reduce transpirational surface area and may therefore enhance water-use efficiency under stressful conditions. Similar reductions in leaf area have been reported in *A. marina* and other mangrove species exposed to prolonged salinity stress and reduced freshwater availability (Li et al., 2023; Beckett et al., 2024). In contrast, the larger leaves observed in Kerala and Goa are consistent with humid environments characterized by higher rainfall and lower evaporative demand, conditions that facilitate greater leaf expansion and carbon assimilation (Reef and Lovelock, 2014; Adams et al., 2023).

Environmental Drivers of leaf trait variation

The strong associations between leaf morphology and hydroclimatic variables indicate that environmental conditions act as important filters shaping trait expression in *A. marina*. Leaf area exhibited positive relationships with temperature, precipitation, and relative humidity, while salinity and tidal amplitude were negatively associated with leaf size and shape index. These results support the view that freshwater availability and salinity are primary determinants of mangrove functional trait variation. Variations in the conditions can influence leaf morphological characteristics by altering physiological and adaptive responses. The differences observed among populations in the present study therefore suggest that leaf traits are closely associated with local climatic conditions and may serve as useful indicators of environmental change and ecosystem resilience (Osland et al. 2023). The observed plasticity of mangrove leaf traits reflects their capacity to adapt to changing environmental conditions while maintaining physiological performance. Previous studies have shown that variations in leaf morphology and chlorophyll content correspond to differences in ecosystem condition, supporting the use of leaf characteristics as sensitive indicators of environmental stress and habitat recovery (Dookie et al. 2023).

Salinity is widely regarded as a dominant environmental constraint in mangrove ecosystems because it influences plant water relations, ion balance, photosynthetic performance, and resource allocation (Naidoo, 1985; Ball and Adams, 2022). Increased salinity often results in reduced leaf expansion and altered biomass allocation patterns as plants invest resources in osmotic adjustment and salt regulation. The strong negative relationship between salinity and leaf size observed in this study is therefore consistent with established physiological responses of mangroves to salt stress. Similarly, tidal amplitude may indirectly influence leaf development by affecting inundation frequency, sediment conditions, nutrient availability, and root-zone oxygen status. Previous studies have demonstrated that variation in inundation regimes can significantly affect leaf functional traits in intertidal plant communities (Zhang et al., 2023).

The positive relationships between leaf area, precipitation, and humidity further highlight the importance of freshwater inputs in supporting morphological development. Freshwater availability reduces osmotic

stress and promotes favourable conditions for leaf expansion, thereby enhancing growth and productivity. Together, these findings demonstrate that hydroclimatic variables are major drivers of leaf morphological variation in *A. marina* across broad environmental gradients.

Population differentiation and ecological significance

Principal component analysis explained 57% of the total morphological variation and revealed clear population-level differentiation, with Gujarat and Kerala populations occupying distinct regions of multivariate trait space. The populations of Gujarat and Kerala occupied distinct regions of multivariate trait space, reflecting the contrasting environmental conditions at opposite ends of the hydroclimatic gradient. Populations from Mumbai, Goa, and Karnataka exhibited intermediate trait characteristics, suggesting responses to transitional environmental conditions.

The observed differentiation likely reflects environmentally induced phenotypic variation and may also indicate potential adaptive divergence among populations. However, because this study relied on field observations, the relative contributions of phenotypic plasticity and genetically based adaptation cannot be conclusively determined. Previous studies have demonstrated considerable plasticity in mangrove functional traits in response to environmental variation, while recent genomic investigations have identified signatures of environmental selection associated with salinity and climatic gradients in *A. marina* (Kennedy et al., 2022; Feng et al., 2023). The morphological patterns observed here therefore provide a useful ecological framework for future studies integrating functional traits with population genomic analyses.

Implications for Wetland Management and Mangrove Conservation

Leaf morphological traits influence key physiological processes, including photosynthesis, transpiration, carbon gain, and water-use efficiency. The significant variation observed among *Avicennia marina* populations along the Indian west coast, with larger leaves in Goa and comparatively smaller leaves in Kerala and Mumbai, reflects phenotypic responses to regional hydroclimatic conditions. Such variation may enhance ecological performance under contrasting environmental settings, with larger leaves favoring resource-rich habitats and smaller leaves improving tolerance to osmotic and hydrological stress.

The sensitivity of leaf morphology to environmental gradients suggests that these traits can serve as useful indicators of habitat condition and ecosystem recovery, supporting restoration monitoring and wetland management (Friess et al. 2024). The observed population-level variation also highlights the importance of using locally adapted planting material in restoration programmes and conserving morphologically distinct populations as potential sources of climate-resilient traits. As future changes in salinity, rainfall, and coastal hydrology are expected to intensify environmental stress, maintaining population-level diversity will be important for climate change adaptation and long-term mangrove conservation (Sasmito et al. 2023; Sippo et al. 2023). Overall, the present findings provide a scientific

basis for restoration planning, conservation prioritization, and evidence-based coastal ecosystem management.

Conclusion

This study demonstrates significant spatial variation in the leaf morphology of *Avicennia marina* along the west coast of India, corresponding to hydroclimatic gradients in salinity, precipitation, humidity, temperature, and tidal amplitude. Populations from the hypersaline environments of Gujarat exhibited smaller and narrower leaves, whereas those from the more humid estuarine regions of Goa and Kerala developed larger leaves, indicating pronounced phenotypic responses to contrasting environmental conditions. Correlation and multivariate analyses further confirmed that leaf morphological traits are strongly associated with hydroclimatic variables and exhibit clear population-level differentiation across the study region.

These findings highlight the importance of hydroclimatic and hydrological factors in shaping leaf trait expression and demonstrate the ecological flexibility of *A. marina* across diverse coastal environments. The observed trait–environment relationships provide a valuable baseline for understanding mangrove responses to environmental change and support the use of locally adapted populations in restoration planning. By linking morphological variation with environmental gradients, this study contributes to mangrove conservation, climate change adaptation, and evidence-based wetland and coastal ecosystem management.

Future Directions

Although the present study provides valuable insights into leaf morphological variation in *Avicennia marina* across a broad hydroclimatic gradient along the west coast of India, several limitations should be acknowledged. First, the study is based on field observations and environmental correlations, which do not allow definitive separation of phenotypic plasticity from genetically based adaptation. The observed morphological differences among populations may reflect environmentally induced trait responses, local adaptation, or a combination of both processes. Second, hydroclimatic variables were compiled from regional datasets and published sources rather than continuous site-specific monitoring, which may not fully capture temporal fluctuations in environmental conditions. In addition, the study focused exclusively on leaf morphological traits and did not incorporate physiological, anatomical, or molecular measurements that could provide deeper insights into adaptive mechanisms. Future research should integrate common-garden and reciprocal-transplant experiments with physiological assessments and population genomic approaches to evaluate the relative contributions of plasticity and genetic differentiation. Combining trait-based analyses with genome-wide markers would improve understanding of adaptive responses to salinity, temperature, and hydrological stress, thereby supporting climate-resilient conservation and restoration strategies for mangrove ecosystems.

Declarations

Competing Interests

The authors declare that they have no financial or non-financial competing interests relevant to the content of this article.

Ethics Approval

All field studies were performed in accordance with national and institutional ethical standards and guidelines for research on natural ecosystems.

Permissions

Field sampling was conducted with prior approval from the State Forest Departments of Gujarat, Maharashtra, Goa, Karnataka, and Kerala, India.

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Author Contribution

A.Sreekanth P.M (Corresponding Author): Conceptualized the study, designed the methodology and Feild InvestigationsB. Thasny KK (First Author): Field investigations, Data curation, Formal Analysis and Manuscript writing.C. Bhavadas N.(Second Author): Result Interpretation and Manuscript revision.

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Data Availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

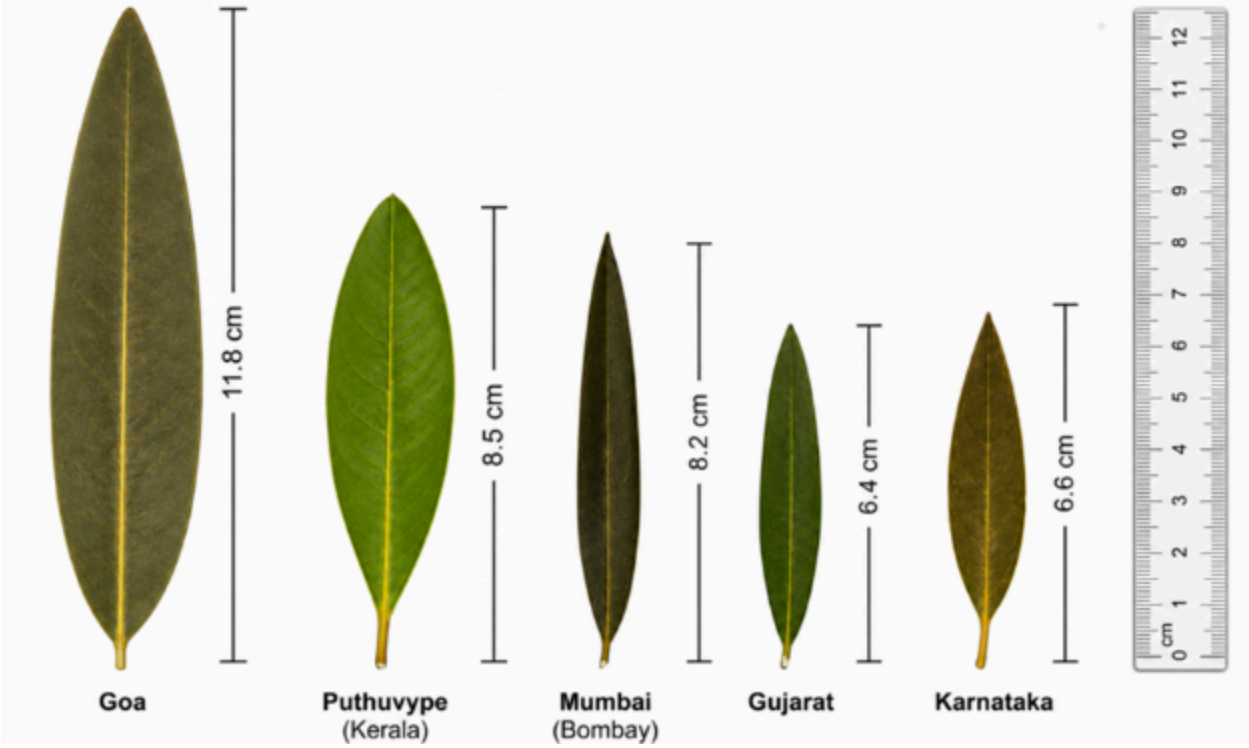


Figure 1

Variation in leaf morphology of *A. marina* across populations

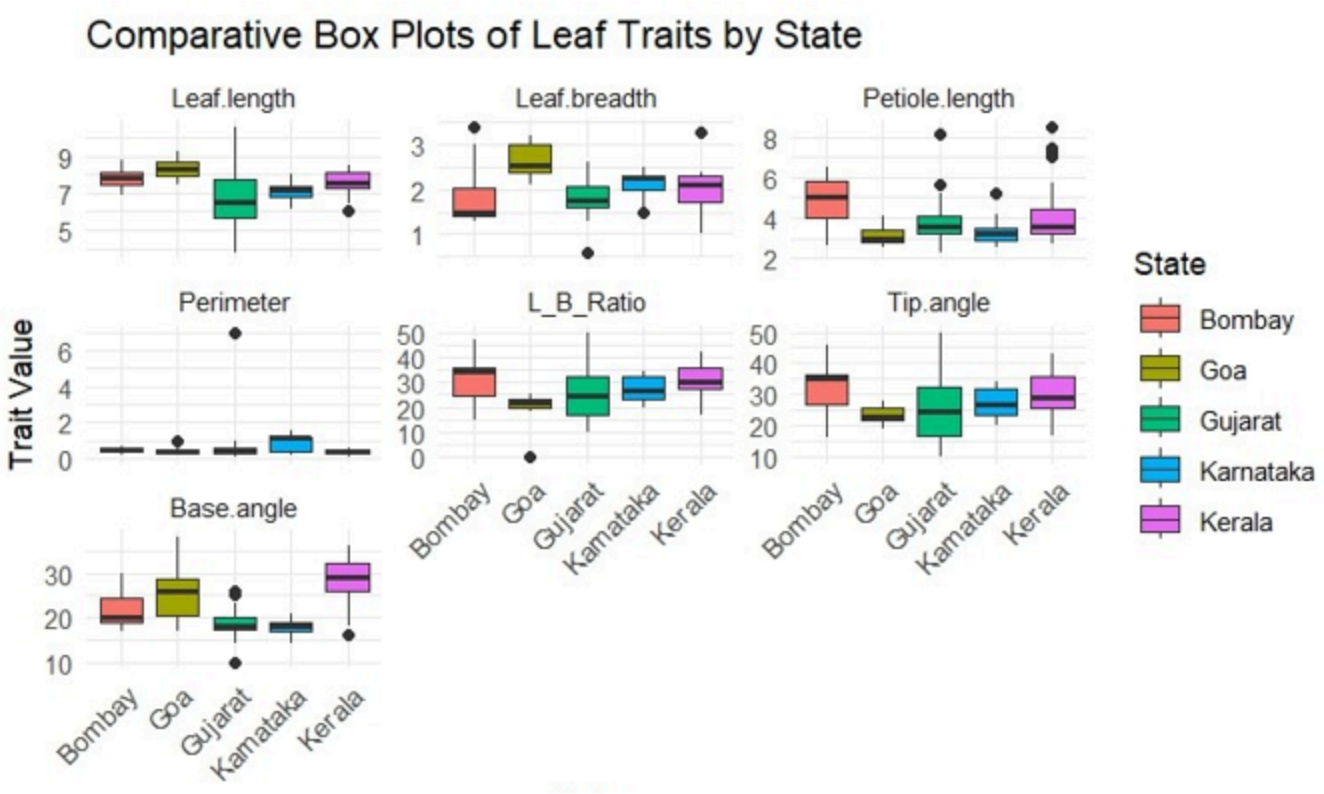


Figure 2

Boxplots showing variation in leaf morphological traits of *A. marina* across five study sites

Traits include (a) Leaf Length (LL), (b) Leaf Width (LW), (c) Petiole Length (PL), (d) Leaf Area (LA), and (e) Leaf Shape Index (LSI). Boxes represent the interquartile range, the horizontal line indicates the median, whiskers denote 1.5 × IQR, and circles represent outliers. Gujarat populations show significantly smaller, narrower leaves, while Kerala and Goa populations display larger, broader leaves. Bombay and Karnataka exhibit intermediate traits.

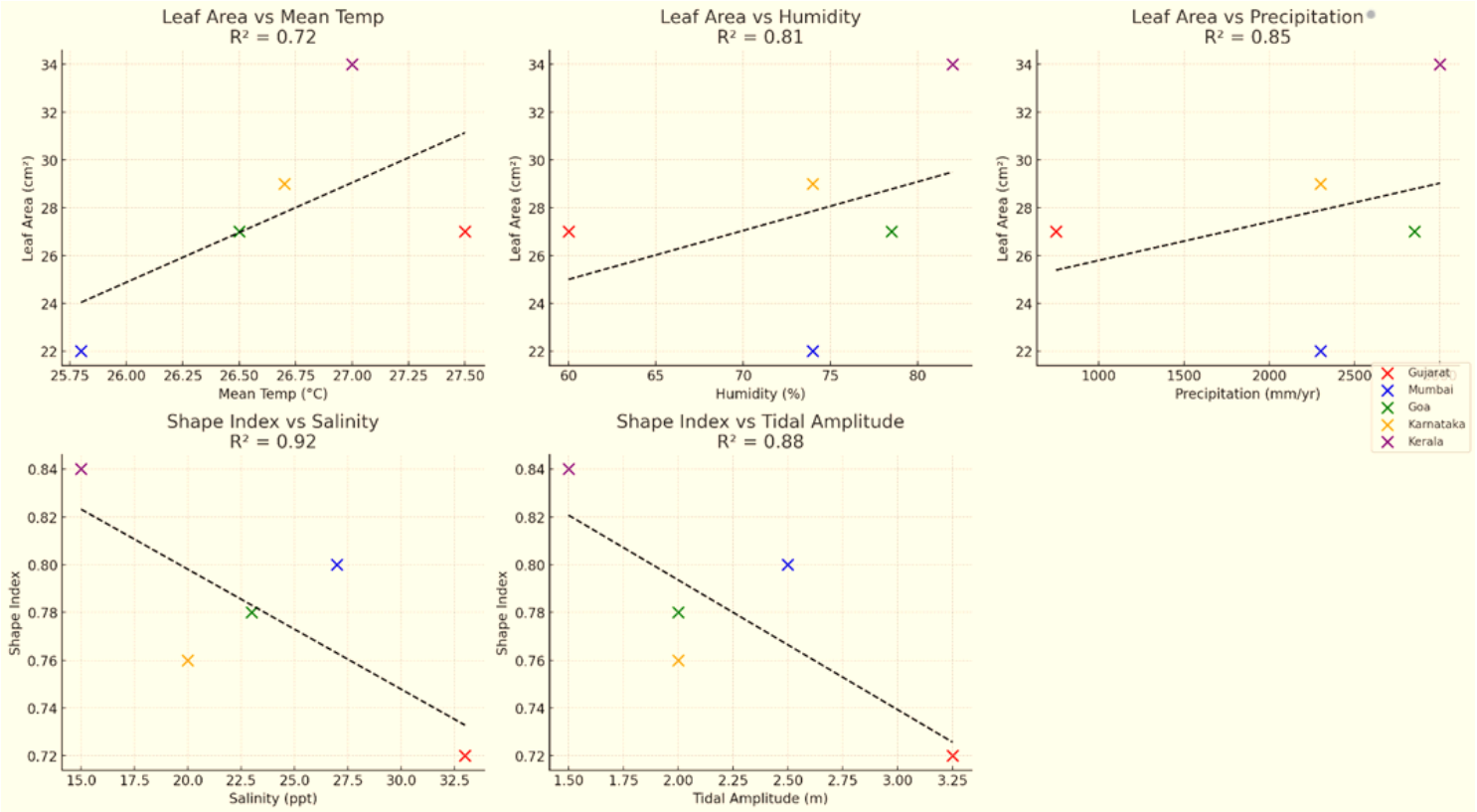


Figure 3

Relationships between hydroclimatic variables and leaf morphological traits in *Avicennia marina*. Leaf area showed positive correlations with mean temperature ($R^2 = 0.72$), relative humidity ($R^2 = 0.81$), and precipitation ($R^2 = 0.85$), whereas shape index was negatively correlated with salinity ($R^2 = 0.92$) and tidal amplitude ($R^2 = 0.88$). Dashed lines indicate linear regression fits.

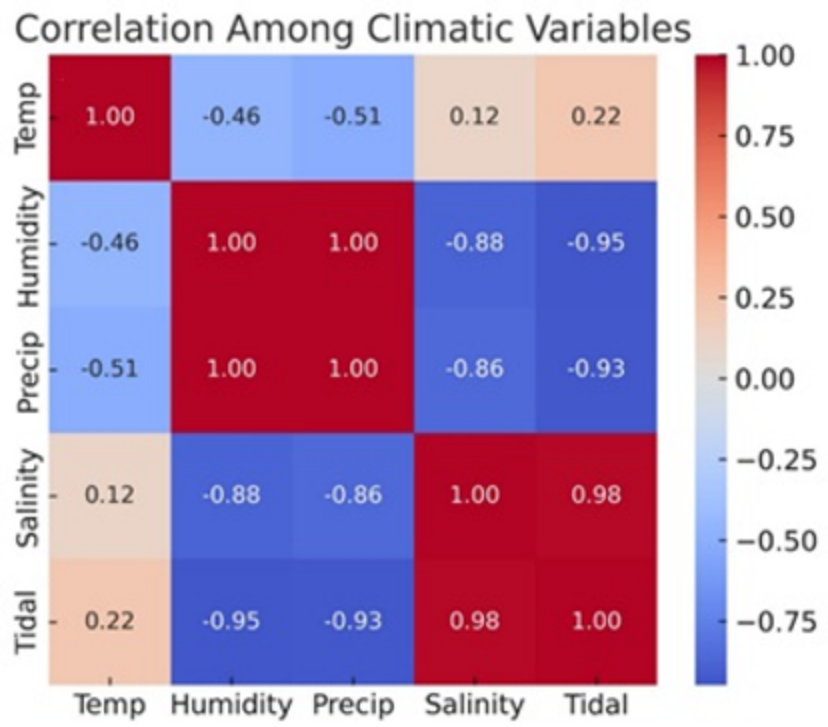


Figure 4

Correlation analysis showed a strong positive relationship between relative humidity and precipitation (r = 1.00). Both variables were strongly negatively correlated with salinity (r = −0.88 and −0.86, respectively) and tidal amplitude (r = −0.95 and −0.93, respectively). Salinity and tidal amplitude exhibited a strong positive correlation (r = 0.98), while temperature showed relatively weak correlations with the other climatic variables (Fig. 4).

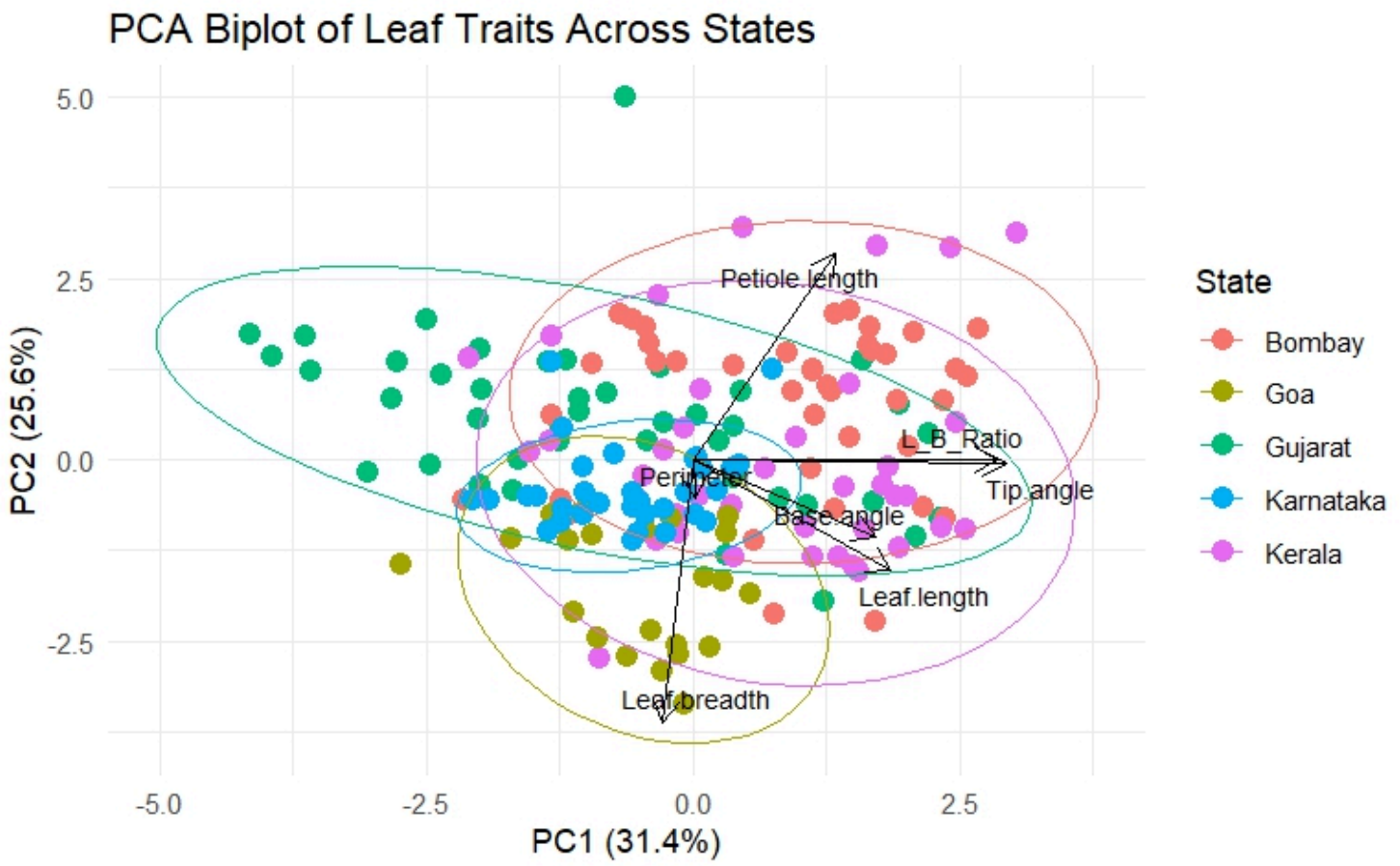


Figure 5

PC1 exhibited strong positive loadings for leaf length, leaf breadth, and petiole length, thereby representing overall leaf size. Populations from Kerala and Bombay were positioned on the positive side of PC1, indicating larger, broader leaves typical of humid coastal environments. In contrast, Gujarat populations clustered on the negative axis of PC1, characterized by narrower and smaller leaves, a pattern consistent with adaptation to arid and saline habitats.PC2 was primarily influenced by base angle, tip angle, and the length-to-breadth (L/B) ratio, reflecting variation in leaf shape. Goa and Karnataka populations occupied intermediate positions, indicating transitional morphologies along the west coast gradient.

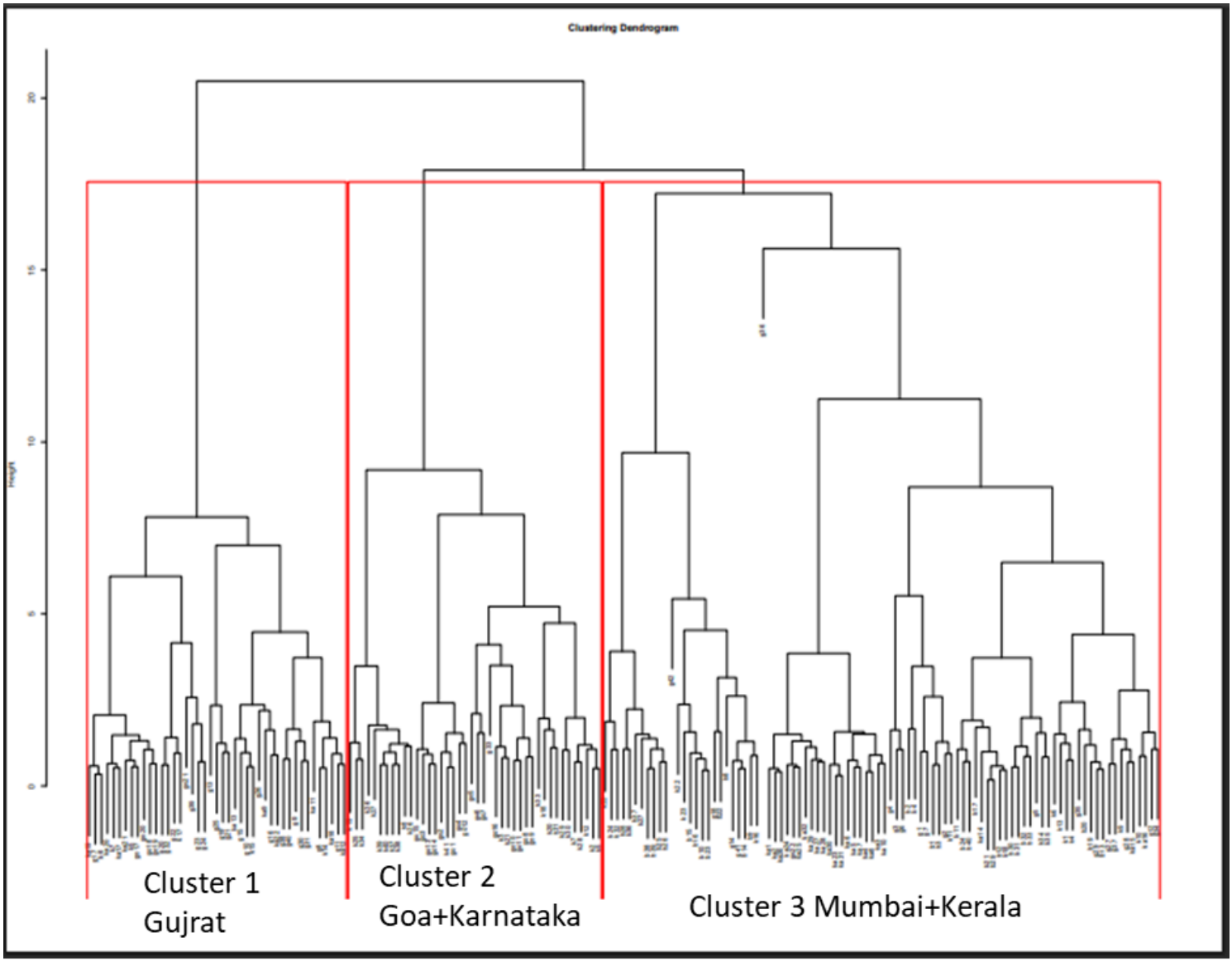


Figure 6

Hierarchical clustering dendrogram of Avicennia marina populations based on leaf morphological traits.Three distinct clusters were observed: Cluster 1 (Gujarat), Cluster 2 (Goa + Karnataka), and Cluster 3 (Mumbai + Kerala). Red vertical lines represent the major cluster divisions.