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Stomatal size and density variation in riparian Araceae along gradient of the Samin River, Central Java, Indonesia

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Abstract. *Wulandari AA, Revalitha AA, Azzam AK, Allobua BSN, Rifki AN, Setyawan AD. 2025. Stomatal size and density variation in riparian Araceae along gradient of the Samin River, Central Java, Indonesia. Cell Biol Dev 9: 78-90.* The riparian zone is a transitional area between aquatic and terrestrial ecosystems, playing a crucial ecological role as a buffer for water quality and as a habitat for biodiversity. The Samin River, located in Central Java, Indonesia, experiences varying abiotic conditions from its upstream to downstream regions, which can influence the biodiversity along its flow. This study aims to assess the diversity of species and the morpho-anatomical characteristics of stomata in plants belonging to the Araceae family across different sections of the Samin River, including the upstream, middle, and downstream areas. Leaf samples were collected through purposive sampling and were analyzed using the replica method to examine stomatal characteristics, such as location, type, shape of guard cells, number of adjacent cells, and stomatal index. A total of 6 species of Araceae were recorded, with species composition changing along the river continuum; only *Xanthosoma sagittifolium* occurred across all reaches and thus enabled within-species comparisons. Stomatal traits in *X. sagittifolium* showed a coordinated shift along the gradient, characterized by smaller stomata accompanied by higher stomatal number and density toward downstream sites. These patterns are consistent with epidermal plasticity and a stomatal size-density trade-off under contrasting environmental conditions across riparian reaches. Overall, the results highlight stomatal traits as sensitive cellular indicators for detecting environmental variation in riparian systems.

Keywords: Adaptation, Araceae, riparian ecosystem, stomata anatomy

INTRODUCTION

River systems are characterized by pronounced longitudinal gradients in abiotic factors such as temperature, light availability, moisture, and substrate composition, which collectively shape the structure and function of riparian vegetation (Nifen et al. 2017; Mukti 2023). These gradients are further intensified by increasing anthropogenic pressures, particularly in tropical regions, where land-use changes along riverbanks can rapidly alter environmental conditions. As a consequence, riparian plants are exposed to spatially heterogeneous and often fluctuating abiotic environments, necessitating effective adaptive mechanisms to maintain physiological stability (Stella and Bendix 2019).

The riparian zone functions as a critical interface between terrestrial and aquatic ecosystems, playing a key role in regulating microclimate, stabilizing riverbanks, and maintaining ecological connectivity (Sholihah and Irawanto 2025). However, alterations in hydrology, sediment dynamics, and water quality along river gradients can disrupt these functions and impose abiotic stress on riparian vegetation (Napoletano et al. 2025)

Plant responses to environmental gradients are often reflected at the anatomical level, where structural modifications contribute to functional adaptation. Among leaf anatomical traits, stomata are particularly important because they directly regulate gas exchange and transpiration, thereby controlling photosynthetic performance and water-use efficiency (Shalsa and Mustakim 2025). Stomatal characteristics, including density, size, and spatial distribution, are highly plastic and responsive to abiotic factors such as light intensity, humidity, and water availability (Julianti et al. 2024). As such, stomatal anatomy represents an integrative and sensitive indicator of plant adaptive responses to long-term environmental conditions, especially in habitats subjected to continuous environmental gradients such as riparian zones (Liu and Zheng 2024).

The Araceae family was selected for this study due to several biologically relevant considerations. Araceae constitutes a dominant and taxonomically diverse group of riparian and semi-aquatic plants in tropical ecosystems, with many species naturally occurring along riverbanks, wetlands, and flood-prone areas (Hartanti et al. 2020). Members of this family exhibit a wide range of leaf morphologies, growth forms, and ecological strategies, suggesting a high degree of anatomical and physiological plasticity. In addition to their ecological role in soil stabilization and erosion control (Jafari et al. 2022), Araceae family are known to tolerate variations in pH, nutrient availability, and environmental pollutants (Croat and Ortiz 2020). This combination of ecological dominance, environmental tolerance, and morphological diversity makes Araceae an ideal model group for examining adaptive variation in stomatal anatomy along environmental gradients.

In Araceae, stomatal size (guard cell/pore dimensions) and stomatal density (number per unit area) jointly constrain potential conductance and frequently exhibit a size density trade off, where higher densities are associated with smaller stomata, potentially supporting efficient regulation under higher evaporative demand, while stomatal complex type tends to be more conserved within species (Chaplin et al. 2024). Accordingly, this study surveys riparian Araceae along the Samin River and characterizes stomatal anatomical features, with a primary focus on testing whether stomatal density and size vary among upstream, midstream, and downstream segments and whether a negative size density association is detectable within species occurring across all segments.

Sungai Samin, located in Central Java, Indonesia, is part of the Bengawan Solo Watershed and extends for approximately 67 km. The river is subject to diverse anthropogenic activities, including agriculture, domestic use, and waste disposal, resulting in marked spatial variability in abiotic conditions along its course (Syahdiba and Kusumandari 2021). These conditions provide a natural environmental gradient that is particularly suitable for investigating anatomical adaptation in riparian plants under real-world ecological pressures.

This study focused on riparian Araceae along a longitudinal gradient of the Samin River (upstream, midstream and downstream gradient). The aim of the study are (i) compiled a species checklist and described species presence or absence patterns and species composition of Araceae in each river section. (ii) Quantified variation in stomatal length, width and density among river sections, with particular emphasis on *Xanthosoma sagittifolium* (L.) Schott, the only species that occurred in all three sections. (iii) Species of *X. sagittifolium* described how changes in stomatal size co-occur with changes in stomatal density along the river gradient. These analyses provide a location specific view of how riparian Araceae adjust stomatal traits along environmental gradients in the Samin River, Central Java, Indonesia.

MATERIALS AND METHODS

Study area and sampling method

Study area

Field sampling was conducted in March 2025 along Sungai Samin, Central Java, Indonesia, a tributary of the Bengawan Solo Watershed (Figure 1). The river exhibits pronounced altitudinal and longitudinal gradients that strongly influence its hydrological characteristics, channel morphology, and riparian vegetation structure. Variations in elevation along the river course from upstream to downstream are closely associated with changes in flow velocity, sediment composition, and riverbank stability, which collectively shape the composition and adaptive strategies of riparian plant communities. The study area and sampling sites were determined using purposive sampling, in which locations and sample objects were deliberately selected based on predefined criteria considered representative of the research objectives (Drupadi et al. 2021).

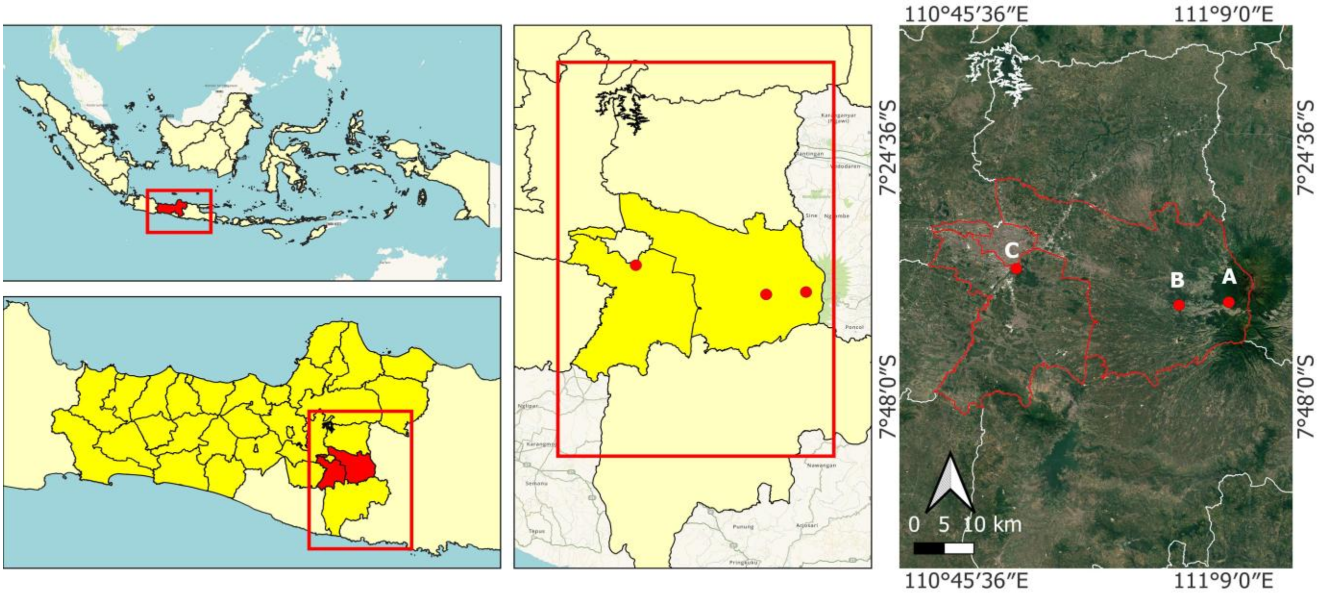

Figure 1. Sampling location points at Samin River, Central Java, Indonesia. A. Upstream (Karanganyar District), B. Midstream (Karanganyar District), and C. Downstream (Sukoharjo District), Central Java, Indonesia

Based on this approach, three river reaches were established to represent distinct fluvial and altitudinal conditions. The upstream gradient, located at approximately 1556 m above sea level (asl) (7°39′3.2076″ S, 111°9′31.158″ E), is characterized by steep terrain, narrow channels, fast-flowing water, and coarse substrates dominated by rocks and gravel. These high-energy fluvial conditions support relatively diverse riparian vegetation, including several species of the family Araceae adapted to cool, moist environments and frequent hydrological disturbance.

The midstream gradient, situated at approximately 615 masl (7°39′17.892″ S, 111°4′55.6104″ E), represents a transitional fluvial zone with moderate channel width, reduced flow velocity, and mixed sediment substrates. This section supports more heterogeneous riparian habitats and accommodates multiple Araceae species with varying ecological tolerances. In contrast, the downstream gradient, located at approximately 88 masl (7°35′57.768″ S, 110°50′0.8052″ E), is characterized by low-gradient topography, wider and deeper channels, dominant fine sediment deposition, and greater anthropogenic influence. These conditions result in simplified riparian vegetation, where only Araceae species with high environmental tolerance are able to persist along the riverbanks.

Sampling method

Sampling was conducted along the Samin River by dividing the study reach into three station namely upstream, midstream, and downstream. In each gradient, a 100 m line transect was established within the riparian zone. At each river gradient (upstream, midstream, downstream), a fixed riparian transect was established and surveyed by walking the transect line. Given that Araceae occurrence was not uniform, plant sampling within transects followed a targeted approach whereby only Araceae individuals encountered along the transect were collected for stomatal analyses.

For each Araceae species encountered in a segment, three individual plants were sampled (n = 3 individuals per species per point found in station), with a minimum spacing between individuals to reduce non-independence due to clumping. From each individual, three leaf of optimal quality was selected for stomatal analysis, prioritizing intact organs, fully expanded leaves, and uniform/optimal leaf size, while avoiding leaves with visible disease symptoms, severe herbivory, or mechanical damage. All samples were coded by species, and individual identity and transported to the laboratory for stomatal impression preparation.

Collected samples were taxonomically identified using *Keanekaragaman Araceae di Pulau Bali* (Kurniawan and Asih 2012) as the primary reference. To preserve tissue integrity and prevent wilting prior to anatomical analysis, leaf samples were placed in plastic bags containing a small amount of water. All samples were subsequently transported to the Biology Laboratory, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret, Surakarta, Central Java, Indonesia, for detailed observation of stomatal anatomy.

Stomata observation

Stomatal observation was initiated by preparing epidermal impressions using the replica method, following the procedure described by Fauziah (2022). Leaf samples were removed from plastic bags and gently cleaned to eliminate surface debris. A thin layer of clear nail polish was then applied evenly to the cleaned leaf surface and allowed to dry completely.

After the nail polish layer had dried, the treated leaf surface was covered with transparent adhesive tape. The tape was carefully peeled off so that the abaxial epidermal layer adhered to the tape surface. The adhesive tape containing the epidermal impression was subsequently mounted onto a glass slide for microscopic examination.

Observations were carried out using a binocular light microscope (Olympus CX31) at 400× magnification. Stomatal observations included the assessment of stomatal type, size, and shape, as well as stomatal number, which was later used for the calculation of stomatal density. This method allowed for consistent visualization and comparison of stomatal morpho-anatomical characteristics among Araceae species across different river gradients.

Stomatal measurement

For each stomata, stomatal length was measured as the linear distance between the outer ends of the two opposing guard cells along the long axis of the pore, whereas stomatal width was measured perpendicular to this axis at the widest part of the guard-cell pair. For each leaf, we measured multiple stomata in randomly selected fields of view and used the mean value per individual as the representative stomatal length and width. For each individual plant, stomatal density was quantified from three fully expanded leaves. For each leaf, three non-overlapping microscopic Fields of Views (FOVs) were selected using a stratified-random approach across the lamina (excluding major veins and leaf margins). Stomatal density was calculated for each FOV and then averaged at the leaf level and subsequently at the individual-plant level prior to statistical analysis.

Stomatal density

Stomatal density was calculated to quantify the number of stomata per unit leaf area based on microscopic observations. Stomatal counts (S) were obtained directly from observations under a light microscope at 400× magnification, and density values were expressed as the number of stomata per square millimeter (stomata /mm²).

The area of the microscopic field of view (A) at 400× magnification was 0.1734 mm², which was used as a constant. Stomatal density was calculated using the following formula (Zhu et al. 2021):

$$Stomatal\ density\ \left(\frac{stomata}{mm^2}\right) = \frac{S}{A}$$

Where:

S: Number of stomata counted within a single microscopic field of view and

A: area per unit area of 400× magnification field of view (0.1734)

Density values were calculated consistently using this formula to allow comparison among observations and sampling sites. For each species and river gradient, stomatal density values derived from microscopic observations were used to obtain representative density values for comparative analysis. Quantitative statistical analysis of stomatal density was conducted only for *X. sagittifolium*, as this species was the only Araceae taxon consistently present across all river gradients (upstream, midstream, and downstream), enabling valid comparison among sites.

Stomatal size

Stomatal length and width (µm) were measured from calibrated images or an ocular micrometer. A consistent measurement definition was applied (e.g., guard-cell complex length and maximum width) across all samples.

Stomatal type and position

Stomatal type and stomatal distribution were identified using standard anatomical criteria. This approach ensured that stomatal density was calculated using a uniform measurement framework, allowing differences observed among river gradients to be interpreted as responses to contrasting environmental conditions rather than methodological variation.

Data analysis

Quantitative data were analyzed using one-way Analysis of Variance (ANOVA) to test for differences in stomatal density among the three Samin River segments (upstream, midstream, and downstream) at a 5% significance level ($\alpha = 0.05$). The biological replicate (n) was defined as an individual plant; for each Araceae species encountered in a segment, three individuals ($n = 3$) were sampled. Stomatal density was quantified on both leaf surfaces (adaxial and abaxial). When multiple technical observations were obtained from the same individual (e.g., several microscopic fields of view and/or repeated impressions), these values were averaged to yield a single mean per individual per leaf surface prior to statistical testing. Individual plants were treated as biological replicates for stomatal measurements. To minimize measurement bias, stomatal counts and size measurements were taken from multiple microscopic fields of view per leaf and averaged at the individual-plant level prior to statistical analysis.

When ANOVA detected a significant effect of river segment, Duncan's Multiple Range Test (DMRT) at 5% was used as a post hoc multiple-comparison test to identify which segment means differed (Sridhar and Charles 2021). Statistical comparisons were conducted only for species present in all three segments, ensuring valid cross-segment inference. For *X. sagittifolium*, one-way ANOVA was used with river section (upstream, midstream, downstream) as a fixed factor and individual plants as replicates.

RESULTS AND DISCUSSION

Diversity of Araceae along the Samin River gradient

The present study documented six genera and six species of the family Araceae distributed along the riparian zone of Sungai Samin, with a clear variation in Araceae presence species across river gradients (Table 1). Differences in species occurrence among the upstream, midstream, and downstream sections indicate that longitudinal river gradients coupled with altitudinal variation play an important role in structuring riparian Araceae communities.

The upstream section (1556 masl) exhibited the highest Araceae presence species, with 4 species recorded. Croat and Ortiz (2020) stated that the higher diversity suggests that upstream riparian environments provide a wider range of suitable microhabitats for Araceae species, which are generally adapted to moist, shaded, and hydrologically dynamic conditions. In montane river sections (upstream line), variations in riverbank stability, substrate composition, and canopy cover are commonly more heterogeneous, potentially allowing species with different ecological requirements such as *Syngonium podophyllum* Schott, *Alocasia odora* (G.Lodd.) Spach, and *Dieffenbachia seguine* (Jacq.) Schott to coexist within a relatively confined area. The presence of multiple Araceae family in the upstream reach indicates that this section may function as an important reservoir of riparian plant diversity.

In the midstream gradient (615 masl), Araceae presence species declined, with 4 species recorded. This section represents a transitional zone along the river continuum, where changes in elevation and river morphology may reduce habitat suitability for species that are restricted to more specific environmental conditions. The persistence of *A. odora* and *X. sagittifolium* in this zone suggests that these species possess broader ecological tolerances compared to other Araceae taxa observed upstream. The midstream reach thus appears to act as an ecotonal zone, where only species capable of adjusting to intermediate riparian conditions are able to persist (O'Donnell 2015).

Table 1. Plants of the Araceae family found on different slopes of the Samin River, Central Java, Indonesia

Gradient	Genus	Species
Upstream	*Syngonium*	*Syngonium podophyllum* Schott
	Alocasia	*Alocasia odora* (G.Lodd.) Spach
	Dieffenbachia	*Dieffenbachia seguine* (Jacq.) Schott
	Xanthosoma	*Xanthosoma sagittifolium* (L.) Schott
Midstream	*Homalomena*	*Homalomena pendula* (Blume) Bakh.f.
	Typhonium	*Typhonium blumei* Nicolson & Sivad.
	Alocasia	*Alocasia odora* (G.Lodd.) Spach
	Xanthosoma	*Xanthosoma sagittifolium* (L.) Schott
Downstream	*Xanthosoma*	*Xanthosoma sagittifolium* (L.) Schott

The downstream section (88 masl) exhibited the lowest diversity, with only one species, *X. sagittifolium*, recorded. This pronounced reduction in Araceae presence species along the lower reach indicates a strong environmental filtering effect, whereby only highly tolerant species remain under downstream conditions. Although specific abiotic variables were not statistically tested in this study, downstream river sections are generally associated with altered hydrological regimes and greater human influence, which may limit the establishment of Araceae species with narrower ecological requirements. The consistent presence of *X. sagittifolium* suggests that this species is particularly well adapted to a wide range of riparian conditions.

The consistent occurrence of *X. sagittifolium* across all river gradients highlights its ecological plasticity within riparian environments. This species may possess morphological and physiological traits that enable it to tolerate variations in elevation, hydrological conditions, and habitat disturbance. In contrast, other Araceae family were restricted to upstream or midstream sections, indicating more limited ecological ranges. Such patterns support the view that species-specific tolerance within Araceae influences their spatial distribution along river gradients.

Overall, the observed decrease in Araceae presence species from upstream to downstream reflects the influence of riverine gradients on riparian plant assemblages. This pattern underscores the importance of upstream riparian zones in maintaining plant diversity and provides an ecological context for subsequent analyses of anatomical traits, such as stomatal characteristics. By documenting how Araceae diversity varies along a river gradient, this study contributes to a better understanding of riparian plant distribution in tropical river systems and establishes a foundation for interpreting adaptive anatomical responses at the species level.

Morpho-anatomical characteristics of stomata

The morpho-anatomical characteristics of stomata in riparian Araceae along the Samin River reveal patterns that are not only species-specific but also ecologically meaningful when interpreted within the context of river gradients. Variations in stomatal position, distribution pattern, number of subsidiary cells, and stomatal type provide insight into how different Araceae family occupy and persist within distinct riparian zones (Table 2).

Stomatal position in relation to river gradient

Stomatal position is a key anatomical trait associated with plant adaptation to environmental conditions (Carlson et al. 2016). In this study, amphistomatic leaves characterized by the presence of stomata on both adaxial and abaxial surfaces were observed in *S. podophyllum*, *D. seguine*, and *H. pendula*, all of which were restricted to the upstream section. This pattern suggests that upstream riparian environments may provide relatively stable moisture conditions that allow greater stomatal exposure without excessive transpirational risk.

In contrast, hypostomatic leaves, with stomata confined to the abaxial surface, were observed in *A. odora*, *Typhonium blumei* Nicolson & Sivad., and *X. sagittifolium*. This anatomical configuration is commonly interpreted as a water-conservation strategy, as it reduces direct exposure of stomata to solar radiation and air movement (Matthews and Lawson 2019; Syabrina et al. 2023). The persistence of hypostomatic species in the midstream and downstream sections suggests that this trait may confer an advantage under riparian conditions where environmental variability and potential water stress are higher.

Stomatal distribution patterns as species-level traits

Two stomatal distribution patterns were identified as amphistomatic and hypostomatic. Amphistomatic was consistently observed in upstream-restricted species (*S. podophyllum*, *D. seguine*, and *H. pendula*), whereas the hypostomatic was observed in species with broader or downstream distributions. Specifically, *A. odora* and *T. blumei* exhibited the hypostomatic, while *X. sagittifolium* displayed the amphibrachyparacytic across all river gradients.

Table 2. Stomata characteristics of the Araceae family found in different gradients of the Samin River, Central Java, Indonesia

Gradient	Species	Stomatal position	Stomatal distribution type	Guard cell shape	Number of subsidiary cell	Stomatal type
Upstream	*Syngonium podophyllum* Schott	Adaxial Abaxial	Amphistomatic	Halter	2	Anomocytic
	Alocasia odora (G.Lodd.) Spach	Abaxial	Hypostomatic	Halter	2	Anomocytic
	Dieffenbachia seguine (Jacq.) Schott	Adaxial Abaxial	Amphistomatic	Halter	2	Anomocytic
	Xanthosoma sagittifolium (L.) Schott	Abaxial	Amphibrachyparacytic	Halter	4	Paracytic
Midstream	*Homalomena pendula* (Blume) Bakh.f.	Adaxial Abaxial	Amphistomatic	Halter	2	Anomocytic
	Typhonium blumei Nicolson & Sivad.	Abaxial	Hypostomatic	Halter	2	Anomocytic
	Alocasia odora (G.Lodd.) Spach	Abaxial	Hypostomatic	Halter	2	Anomocytic
	Xanthosoma sagittifolium (L.) Schott	Abaxial	Amphibrachyparacytic	Halter	4	Paracytic
Downstream	*Xanthosoma sagittifolium* (L.) Schott	Abaxial	Amphibrachyparacytic	Halter	4	Paracytic

The consistency of these patterns across gradients indicates that stomatal distribution in Araceae is primarily species-determined rather than environmentally plastic. However, the fact that species with amphistomatic-hypostomatic stomata dominate midstream and downstream sections suggests that this distribution pattern may be better suited to a wider range of riparian conditions. Thus, while the trait itself is taxonomically stable, its ecological significance becomes apparent when viewed in relation to species distribution along the river gradient.

Guard cell morphology and subsidiary cells

All observed Araceae species possessed halter-shaped guard cells, reflecting a conserved anatomical feature within the family (Spiegelhalder and Raissig 2021; Akbar et al. 2023). This uniformity underscores the taxonomic coherence of Araceae and suggests that guard cell shape alone does not explain differences in species distribution along the river.

In contrast, variation in the number of subsidiary cells appears to have greater functional relevance. Most species exhibited two subsidiary cells, whereas *X. sagittifolium* consistently showed four subsidiary cells across all gradients. Subsidiary cells are known to facilitate osmotic regulation and influence the dynamics of stomatal opening and closing (Gray et al. 2020; Cambaba and Kasi 2022). The presence of four subsidiary cells in *X. sagittifolium* may enhance stomatal control, potentially contributing to its ability to maintain physiological function under a wide range of riparian conditions. This anatomical feature may therefore play a role in the broad ecological distribution of *X. sagittifolium* along Sungai Samin.

Stomatal type and ecological implications

Two stomatal types were identified among the studied species, namely anomocytic and paracytic. Anomocytic stomata were observed in 5 species, most of which were restricted to upstream or midstream gradient. In contrast, *X. sagittifolium* consistently exhibited paracytic stomata across all gradients. Paracytic stomata, characterized by subsidiary cells aligned parallel to the guard cells, are often associated with more efficient stomatal regulation (Pautov et al. 2021). The stability of stomatal type in *X. sagittifolium* across contrasting river sections suggests that this trait is a fixed anatomical characteristic rather than an environmentally induced response. When considered alongside its distribution across all gradients, the presence of paracytic stomata reinforces the interpretation that *X. sagittifolium* possesses anatomical features that support ecological versatility in riparian habitats.

Integration with gradient structure and subsequent quantitative analysis

Although the morphoanatomical traits described above do not vary within species across gradients, their distribution among species provides an important framework for understanding patterns of Araceae species presence along Samin River. Upstream gradient support species with amphistomatic leaves and predominantly anomocytic stomata, while midstream and downstream sections are dominated by species with hypostomatic leaves and, in the case of *X. sagittifolium*, paracytic stomata.

These qualitative anatomical patterns establish a structural context for subsequent quantitative analyses of stomatal density. In particular, the wide distribution and distinctive stomatal traits of *X. sagittifolium* justify its selection as the focal species for quantitative comparison across river gradients, linking anatomical structure to functional responses in riparian environments.

Morphoanatomical characteristics of abaxial stomata based on microscopic observation

Microscopic observations of abaxial leaf epidermis at 400× magnification (Figure 2) provide direct visual confirmation of the stomatal characteristics summarized in Table 2. Across the six Araceae species examined, clear differences were observed in stomatal type, arrangement of subsidiary cells, and integration of stomatal complexes within the epidermal tissue, reflecting species-specific anatomical traits rather than gradient-induced plasticity.

General stomatal architecture in Araceae

In five of the six species (*A. odora*, *D. seguine*, *H. pendula*, *S. podophyllum*, and *T. blumei*; Figures 2.A-E), stomata are characterized by guard cells (sp) forming a distinct stomatal pore (ps) that is surrounded by epidermal cells (se) without morphologically specialized subsidiary cells (st). This configuration corresponds to the anomocytic stomatal type, in which stomata appear embedded within a relatively homogeneous epidermal matrix. The consistency of this stomatal architecture across multiple genera indicates that anomocytic stomata represent a dominant and conserved anatomical pattern within riparian Araceae. From a functional perspective, the integration of stomata within undifferentiated epidermal cells may support stable gas exchange while minimizing structural complexity. This stomatal configuration is commonly associated with taxa that occupy moist or shaded habitats, such as riparian environments, where extreme regulation of stomatal aperture may be less critical (Song et al. 2020).

Distinctive stomatal complex in Xanthosoma sagittifolium

In contrast to the anomocytic pattern observed in most species, *X. sagittifolium* (Figure 2.F) exhibits a clearly differentiated paracytic stomatal type, characterized by the presence of subsidiary cells (st) arranged parallel to the guard cells (sp). This configuration forms a more complex stomatal apparatus compared to the other Araceae species examined. Importantly, the paracytic stomatal structure of *X. sagittifolium* is consistently observed across upstream, midstream, and downstream sections of the Samin River, as indicated in Table 2. This consistency suggests that stomatal type in this species is a stable, species-specific anatomical trait, rather than a response to local environmental variation. The presence of well-defined subsidiary cells may enhance stomatal regulation efficiency, providing *X. sagittifolium* with greater physiological flexibility under a broad range of riparian conditions.

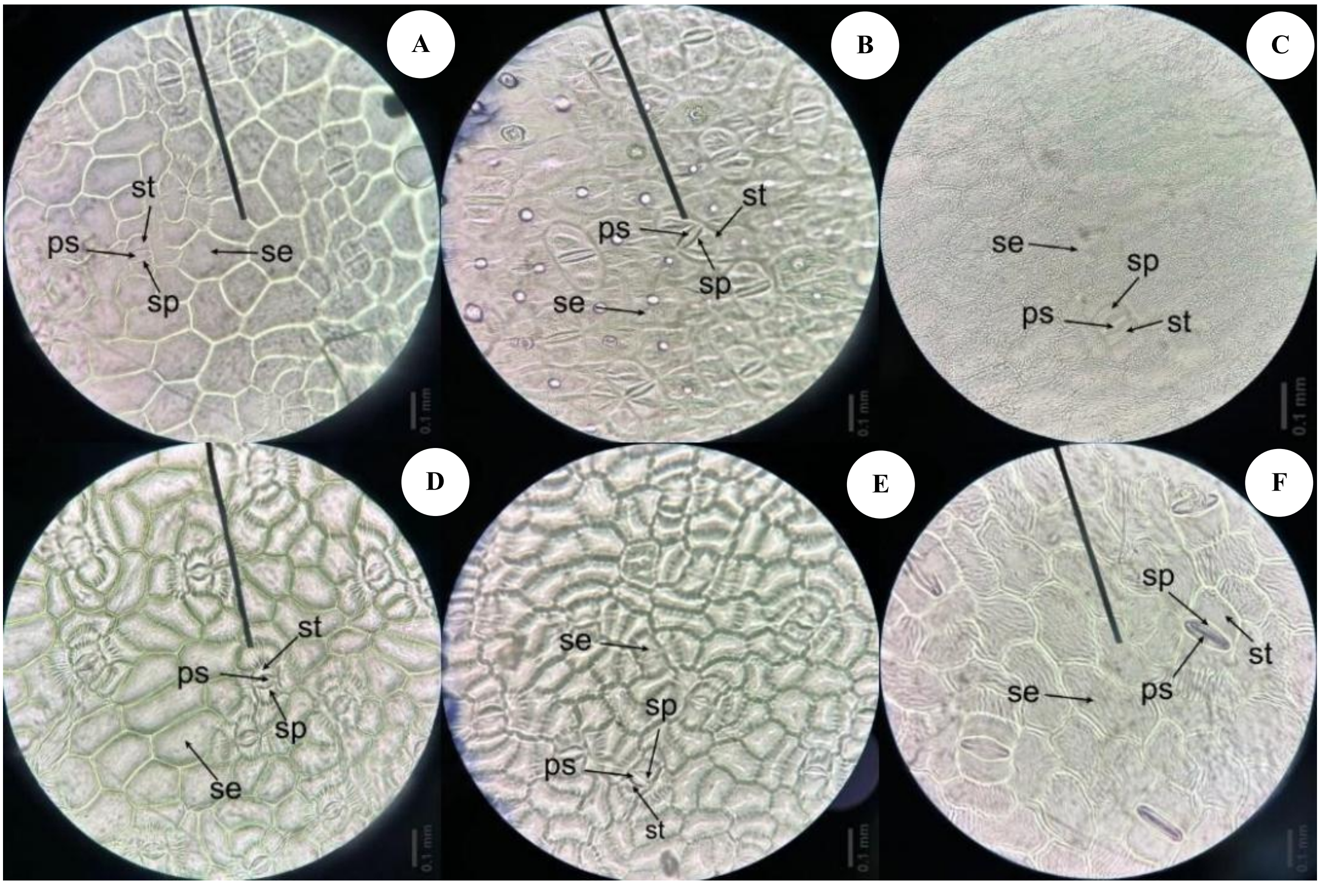

Figure 2. Anatomy of abaxial stomata of leaf, magnification 400x. A. *Alocasia odora*, B. *Dieffenbachia seguine,* C. *Homalomena pendula,* D. *Syngonium podophyllum*, E. *Typhonium blumei,* F. *Xanthosoma sagittifolium*. Note: ps: stomata pore, sp: guard cell, st: subsidiary cell, se: epidermis cell (Author documentation 2025)

Integration with river gradient and species distribution

Although the microscopic observations do not indicate within-species variation in stomatal structure along the river gradient, they provide important context for understanding species distribution patterns. Species restricted to the upstream section predominantly exhibit anomocytic stomata, whereas *X. sagittifolium*, which occurs along the entire river gradient, possesses a more complex paracytic stomatal apparatus. This pattern suggests that while stomatal morphology itself is taxonomically conserved, certain anatomical configurations such as the paracytic type may be associated with broader ecological tolerance in riparian environments.

The midstream and downstream gradient of Samin River are represented by fewer Araceae family, with *X. sagittifolium* as the most commonly found species. The persistence of this species across all gradients, together with its distinctive stomatal architecture, highlights the potential role of stomatal complex structure in supporting wide habitat occupancy.

Relevance to subsequent quantitative analysis

The visual differentiation of stomatal types observed in Figure 2 supports the rationale for focusing quantitative analyses of stomatal density on *X. sagittifolium*. Because this species shows a qualitatively consistent stomatal complex across all river sections, the anatomical observations suggest that subsequent differences in stomatal density among sections are suggest that subsequent differences in stomatal density among sections are consistent with environmental responses of a single stomatal type, rather than being driven by changes in stomatal type itself. However, our observational design cannot fully separate adaptive, plastic, and other sources of variation.

Stomatal size variation and its implications along the Samin River gradient

Stomatal characteristics of riparian Araceae along the Samin River showed clear variation in stomatal size, expressed as pore length and width, among species and river gradients (Table 3). Stomatal size is an important anatomical trait because it influences gas exchange capacity, transpiration regulation, and plant adaptation to environmental conditions (Smith et al. 2023). In this study, variation in stomatal size is interpreted within the context of the longitudinal riparian gradient of Samin River, which integrates changes in elevation, microclimate, and riverine environmental conditions.

Table 3. Stomata size in Araceae family found in different Samin River gradients, Central Java, Indonesia

Gradient	Species	Adaxial surface		Abaxial surface	
		Length (µm)	Width (µm)	Length (µm)	Width (µm)
Upstream	*Syngonium podophyllum* Schott	63.23	40.12	67.45	43
	Alocasia odora (G.Lodd.) Spach	-	-	57.5	33.45
	Dieffenbachia seguine (Jacq.) Schott	92.44	24.2	84.5	34.6
	Xanthosoma sagittifolium (L.) Schott*	-	-	110.98±0.94^{a}	60±2.10^{a}
Midstream	*Homalomena pendula* (Blume) Bakh.f.	60.55	32.4	88.87	40.6
	Typhonium blumei Nicolson & Sivad.	-	-	76.00	42.4
	Alocasia odora (G.Lodd.) Spach	-	-	44.76	26.78
	Xanthosoma sagittifolium (L.) Schott*	-	-	88.76±0.94^{b}	42.45±1.04^{b}
Downstream	*Xanthosoma sagittifolium* (L.) Schott*	-	-	55.89±0.95^{c}	34.9±0.98^{c}

Note: Numbers with the same letters indicate no significant difference ($P>0.05$) according to the 5% DMRT test, the * sign indicates species found throughout the Samin River gradient

Variation in stomatal size among species and gradients

Based on Table 3, stomatal size varied markedly among species and sampling gradients, particularly on the abaxial leaf surface, which represents the functional surface for gas exchange in all observed taxa. The largest stomata were recorded in *X. sagittifolium* from the upstream gradient, with a stomatal length of 110.98 µm and width of 60 µm, whereas the smallest stomata were observed in *A. odora* from the midstream gradient, with a length of 44.76 µm and width of 26.78 µm.

Species occurring exclusively in the upstream gradient, such as *S. podophyllum* and *D. seguine*, generally exhibited relatively larger stomatal dimensions compared to species recorded in the middle and downstream sections. This pattern suggests that upstream riparian environments of Sungai Samin, which are characterized by cooler temperatures and higher moisture availability, may permit the development of larger stomatal pores without incurring excessive transpirational costs.

Interpretation of DMRT results

Differences in stomatal size among gradients for *X. sagittifolium* were supported by DMRT analysis, where values marked with different letters indicate statistically significant differences at $P<0.05$. Importantly, this statistical comparison is biologically meaningful only for *X. sagittifolium*, as it is the sole species recorded consistently across upstream, midstream, and downstream sections (Table 3). For other species, which were restricted to one or two gradients, statistical comparison across gradients is not applicable and therefore not interpreted.

Duncan's Multiple Range Test (DMRT) at the 5% significance level revealed significant differences in stomatal length and width of *X. sagittifolium* on the abaxial leaf surface among river gradients ($P<0.05$), with the highest values observed upstream and the lowest downstream.

The observed variation in stomatal size among Araceae family reflects morphological adaptation within a riverine riparian system, where environmental conditions change longitudinally along the river rather than solely with elevation. Larger stomata in upstream riparian zones may enhance gas exchange efficiency under humid and cooler conditions, whereas smaller stomata in midstream and downstream sections may contribute to tighter regulation of water loss under warmer and potentially more variable riparian environments (Bucher et al. 2017).

Table 3 shows a consistent and statistically supported upstream and downstream shift in stomatal size of *X. sagittifolium* along the Samin River continuum. Based on three individuals per river section ($n = 3$) and separation by DMRT at $\alpha = 0.05$, stomata on the abaxial leaf surface were significantly larger upstream and progressively smaller toward downstream reaches: mean stomatal length decreased from 110.98 µm (upstream) to 88.76 µm (midstream) and 55.89 µm (downstream), while mean stomatal width declined from 60.00 µm to 42.45 µm and 34.90 µm, respectively. This monotonic pattern indicates a strong association between longitudinal river position (upstream to downstream) and stomatal dimensions in this species, suggesting systematic variation in leaf epidermal traits along the gradient. Importantly, because comparisons are derived from samples collected within one sampling area per section (i.e., without independent site replication within each section), the differences should be interpreted as location-specific patterns along the studied river gradient, rather than definitive section-level effects generalizable to all upstream, midstream, and downstream habitats.

By integrating stomatal size variation with species distribution along Samin River, this study demonstrates that stomatal traits in Araceae are shaped by both species-specific characteristics and river-gradient-related environmental constraints. The consistent presence and measurable stomatal size variation of *X. sagittifolium* across all gradients further support its role as a key species for understanding stomatal adaptation in riparian ecosystems.

Stomatal number and density along the river gradient

Table 4 shows that stomatal number and density of riparian Araceae family vary among species and river gradients, with stomata predominantly occurring on the abaxial leaf surface. In several species, the adaxial surface completely lacked stomata, as indicated by the absence symbol (-). This pattern reflects a common adaptive strategy in tropical riparian plants, in which abaxial stomatal placement reduces direct exposure to solar radiation and minimizes excessive transpirational water loss.

Species such as *A. odora*, *T. blumei*, and *X. sagittifolium* consistently exhibited hypostomatic leaves across all sampling locations, supporting the morpho-anatomical characteristics described previously. In contrast, *S. podophyllum* and *D. seguine* possessed stomata on both adaxial and abaxial surfaces; however, in these species, stomatal number and density were markedly higher on the abaxial surface. This indicates that, even in amphistomatic species, the lower epidermis functions as the primary site for regulating gas exchange. In *X. sagittifolium*, stomatal size decreased while stomatal density increased from the upstream to the downstream section, indicating a co-variation between stomatal size and density that is consistent with a size-density trade-off along the sampled sites of the Samin River.

Table 4 shows that stomatal deployment in *X. sagittifolium* differs significantly along the upstream-midstream-downstream continuum of the Samin River. Using individual plants as biological replicates (n = 3 per river location/section) and based on DMRT at α = 0.05, both the mean stomatal number per microscopic field of view and the area-standardized stomatal density ($/mm^2$) on the abaxial leaf surface increased monotonically from upstream to downstream. Mean stomatal number increased from 4.3^{a} (upstream) to 16.7^{b} (midstream) and 33.5^{c} (downstream), while stomatal density rose from $24.86^{a}/mm^2$ to $96.53^{b}/mm^2$ and $193.64^{c}/mm^2$. Because stomatal density is derived by standardizing field-based counts to a fixed observation area, the concurrent increase in both metrics indicates a consistent downstream increase in stomatal packing on the abaxial epidermis across the sampled locations.

For other species, including *A. odora* and *T. blumei*, variation in stomatal number and density among locations is evident in Table 4, however, no statistical comparison across gradients is inferred because these species were not present at all sampling sites. Consequently, differences observed in these taxa are interpreted descriptively and reflect species-specific responses within particular sections of the river.

When interpreted together with stomatal size variation (Table 3) and stomatal morpho-anatomical traits (Table 2 and Figure 2), the pattern observed in *X. sagittifolium* suggests a coordinated adjustment of stomatal traits along the Samin River riparian continuum. Specifically, the increase in stomatal number and density toward downstream sections occurs concurrently with a reduction in stomatal size, indicating a functional balance between gas exchange capacity and transpirational control under changing riparian environmental conditions.

Abiotic variation and stomatal anatomical adjustments in riparian Araceae along the Samin River

Altitudinal variation along the riparian zone of the Samin River appears to be a primary driver of environmental heterogeneity that is reflected in stomatal trait variation within Araceae. As stated by Kumar et al. (2020) that altitude is a major limiting factor that affects various other abiotic parameters such as temperature, rainfall, wind profile, light intensity and duration, physiographic factors, as well as soil fauna and flora. Consistent with this framework, our field measurements show a marked decline in elevation from upstream (1556 masl) to downstream (88 masl), accompanied by pronounced shifts in microclimatic and physicochemical conditions.

Light intensity increased from 2942 lux (upstream) to 6022.7 lux (downstream), while air temperature rose from 23.6°C to 33°C; similar increasing trends were observed for water temperature (23.4°C to 33.9°C) and soil temperature (20.3°C to 33°C). These segment-level patterns indicate that downstream habitats are substantially warmer and more highly irradiated than upstream sites, conditions that can elevate transpirational demand and intensify the need to sustain efficient CO_2 diffusion for photosynthesis.

In this context, stomatal traits can be interpreted as functional adjustments to differing abiotic regimes along the river continuum. Kumar et al. (2020) note that in lowlands (downstream), light intensity and temperature tend to be high, so plants experience increased demands for transpiration and photosynthesis. This condition drives adaptation in the form of increased stomatal number and density to maintain physiological efficiency.

Table 4. Number and density of stomata per unit area of the surface view microscope

Gradient	Species	Mean of stomata number		Stomata density ($/mm^2$)	
		Adaxial	Abaxial	Adaxial	Abaxial
Upstream	*Syngonium podophyllum* Schott	6.6	10.6	38.15	61.27
	Alocasia odora (G.Lodd.) Spach	-	8.6	-	49.71
	Dieffenbachia seguine (Jacq.) Schott	1.3	9.6	7.51	55.49
	Xanthosoma sagittifolium (L.) Schott*	-	4.3 ± 0.5^{a}	-	24.86 ± 2.89^{a}
Midstream	*Homalomena pendula* (Blume) Bakh.f.	1	4.3	5.78	24.86
	Typhonium blumei Nicolson & Sivad.	-	12.6	-	72.83
	Alocasia odora (G.Lodd.) Spach	-	13.5	-	78.03
	Xanthosoma sagittifolium (L.) Schott*	-	16.7 ± 2.64^{b}	-	96.53 ± 15.29^{b}
Downstream	*Xanthosoma sagittifolium* (L.) Schott*	-	33.5 ± 2.29^{c}	-	193.64 ± 71.46^{c}

Note: Numbers with the same letters indicate no significant difference (P>0.05) according to the 5% DMRT test, the * sign indicates species found throughout the Samin River gradient

This results align with this expectation, particularly for *X. sagittifolium*, which was recorded across the entire gradient and exhibited a strong increase in stomatal abundance from upstream (4.3 stomata; 24.86/mm²) to downstream (33.5 stomata; 193.64/mm²). Such a pattern is compatible with adaptive or plastic shifts toward higher stomatal densities in warmer and brighter downstream conditions, potentially supporting higher photosynthetic demand while maintaining tighter control over water loss.

Beyond microclimate, downstream segments also differed in water chemistry. TDS increased downstream (Table 5), indicating a higher concentration of dissolved substances in the water column and potentially in adjacent riparian substrates. Elevated dissolved solutes may alter osmotic conditions and influence plant water relations indirectly, particularly for riparian taxa whose root zones interact with near-river soils or periodically saturated substrates. In parallel, water pH remained alkaline but decreased slightly downstream, suggesting longitudinal variation in carbonate chemistry and ionic composition. Although the present study does not quantify ion identity or salinity stress explicitly, the combined increase in TDS and shift in pH provide additional evidence that downstream habitats differ physicochemically from upstream reaches. These physicochemical contrasts can contribute to habitat filtering, potentially affecting growth conditions and thereby influencing the expression of leaf functional traits, including stomatal density and size, across the gradient.

Other measured parameters support the presence of environmental constraints that may intensify toward downstream. Dissolved Oxygen (DO) declined markedly from upstream to downstream (10.6 ppm to 5.8 ppm) while soil pH decreased from 6.3 to 5.3, indicating increasingly acidic soils. Such changes may influence riparian plant performance through root-zone chemistry and oxygen availability in wet substrates, which can feed back on whole-plant water status and stomatal regulation. Conversely, upstream sites at higher elevation are characterized by cooler conditions, which generally reduce evaporative demand. This aligns with the statement that in upstream gradient (1556 masl), a cooler and more humid environment reduces transpiration requirements, so plants may have fewer but larger stomata (Kumar et al. 2020).

Table 5. Abiotic factor measurement along Samin River, Central Java, Indonesia

Abiotic factor	Upstream	Midstream	Downstream
Light intensity (lux)	2942	3012	6022
Elevation (masl)	1556	615	88
Air temperature (°C)	23	26	33
Water temperature (°C)	23	27	34
Soil temperature (°C)	20.3	24.3	33
Water pH	9.3	9.1	8.8
Soil pH	6.5	6.3	5.3
TDS (ppm)	1630	1830	1860
DO (ppm)	11	10.6	5.8

Accordingly, longitudinal changes in stomatal parameters can be viewed as a coordinated morphological-physiological response to abiotic variation structured by elevation, with downstream conditions favoring stomatal configurations that sustain gas exchange under higher thermal and radiative loads.

Overall, the present findings support the interpretation that stomatal traits serve as useful indicators of plant responses to environmental gradients where the changes in stomatal parameters constitute a plant response to differences in abiotic conditions influenced by altitude (Kumar et al. 2020). The downstream increase in stomatal density together with the general expectation of stomatal size density coordination under higher light and temperature suggests epidermal trait adjustment along the river gradient. The occurrence of multiple stomatal distribution patterns (e.g., amphistomatic and hypostomatic) and stomatal complex types (e.g., anomocytic and paracytic) across Araceae further indicates diversity in anatomical strategies within the riparian community, while *X. sagittifolium* emerges as the most environmentally tolerant species due to its presence across all segments. These results underscore the value of stomatal morphological variation for interpreting plant adaptation/plasticity along riverine gradients and can inform riparian conservation planning under changing abiotic conditions.

Stomatal plasticity and adaptive in riparian Araceae

Stomatal plasticity represents a fundamental adaptive mechanism through which plants modulate cellular structure and function in response to environmental heterogeneity (Lachowiec et al. 2016). In riparian Araceae along the Samin River, stomatal plasticity is expressed through coordinated variation in stomatal distribution, morphology, size, and density, indicate adaptive strategies operating at the cellular level rather than merely shifts in species composition along the river gradient. The riparian gradient of the Samin River (upstream-midstream-downstream) imposes longitudinal variation in microclimatic and hydrological conditions that act as selective pressures on stomatal traits. Figure 3 illustrates a coordinated stomatal size-density trade-off, particularly evident in *X. sagittifolium*, where larger stomata with lower density dominate upstream environments, while smaller stomata with higher density prevail downstream. This conceptual framework integrates quantitative findings on stomatal size and stomatal density into a unified model of adaptive cellular plasticity.

Results from this study further indicate that certain stomatal traits such as stomatal type, guard cell shape, and subsidiary cell arrangement remain relatively conserved within species (Table 2), suggesting strong genetic and developmental control. In contrast, stomatal size and density show substantial variability along the river gradient, indicating that these traits possess higher phenotypic plasticity and serve as primary adjustment mechanisms in response to changing riparian conditions. The strongest expression of stomatal plasticity was observed in *X. sagittifolium*, the only species recorded across all river gradients. In this species, a progressive reduction in stomatal size from upstream to downstream was accompanied by a statistically significant increase in stomatal number and density. From a cellular perspective, smaller stomata are associated with faster opening and closing dynamics due to reduced guard cell volume, allowing finer regulation of pore aperture under fluctuating environmental conditions. The increase in stomatal density thus compensates for reduced pore size, maintaining effective gas exchange while enhancing transpirational control.

The abaxial stomatal micrographs (Figure 4) further support this interpretation by demonstrating that, despite quantitative variation in size and density, the basic stomatal architecture remains conserved across species. Guard cells, subsidiary cells, and epidermal cells exhibit consistent structural organization, indicating that adaptive responses in riparian Araceae primarily involve quantitative modulation of stomatal traits rather than fundamental anatomical restructuring.

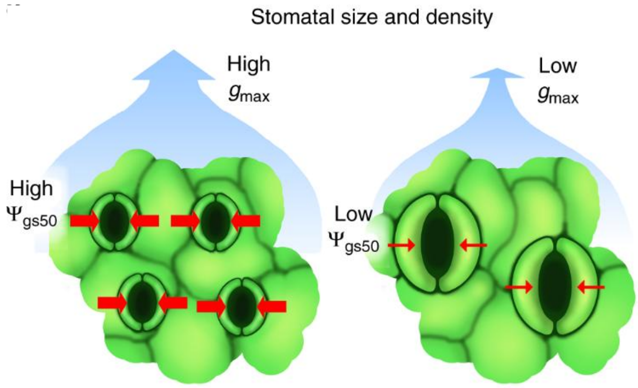

Figure 3. Conceptual framework of stomatal plasticity and adaptive strategies in riparian Araceae along an environmental gradient

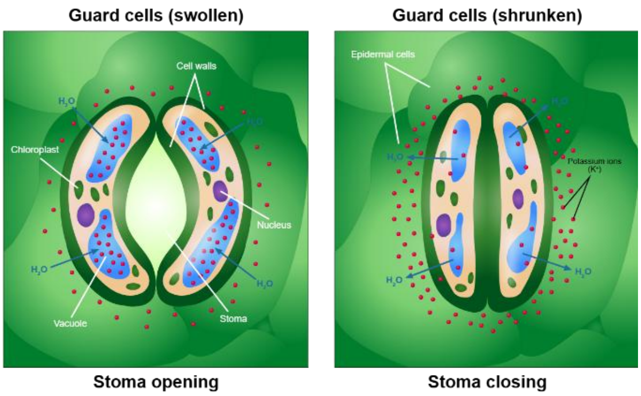

Figure 4. Cellular mechanisms of stomatal opening and closing as adaptive responses in riparian Araceae

Species restricted to upstream or midstream gradients exhibit more conservative stomatal configurations, with limited variation in stomatal size or density. This suggests narrower ecological tolerance ranges and reduced plastic capacity compared to *X. sagittifolium*. Such differences highlight the importance of stomatal plasticity in enabling certain species to persist across heterogeneous riparian environments. The integration of quantitative stomatal data with morpho-anatomical observations demonstrates that adaptive strategies in riparian Araceae are driven by fine-scale cellular adjustments, particularly in stomatal size and density. This form of plasticity allows plants to balance carbon acquisition and water conservation along the dynamic riparian gradient of the Samin River, reinforcing the role of stomatal traits as key indicators of adaptive capacity at the cellular level.

Species and community responses

Patterns observed in stomatal traits of riparian Araceae along the Samin River reveal a clear distinction between community-level trends and specific species adaptive responses. At the community level, Araceae presence species declined markedly from upstream to downstream gradients, with 4 species recorded in the upstream station, fewer species in the midstream, and only a single species present in the downstream section. This pattern indicates that the riparian gradient functions as an ecological filter, limiting species persistence toward lower sections of the river.

However, when stomatal traits are examined at the species level, particularly from an anatomical and cellular perspective, adaptive responses are not uniformly expressed across the community. Instead, stomatal plasticity is strongly species-dependent, with only certain taxa exhibiting the capacity to adjust stomatal traits across environmental gradients. This distinction is most evident in *X. sagittifolium*, the only species encountered consistently across all river gradients. Unlike other species that were restricted to one or two sections, *X. sagittifolium* demonstrated statistically supported variation in stomatal size, number, and density along the riparian gradient. The presence of this species across contrasting environments suggests a broader ecological amplitude supported by high stomatal plasticity at the cellular level.

In contrast, species such as *A. odora*, *T. blumei*, *S. podophyllum*, and *D. seguine* exhibited more conservative stomatal configurations. Although these species displayed distinct stomatal morphologies and densities within specific river sections, their restricted distribution limited their capacity for cross-gradient comparison. This pattern suggests that these taxa may rely on fixed anatomical traits optimized for narrower environmental conditions, rather than flexible stomatal adjustment mechanisms.

From a developmental and cellular standpoint, these findings highlight that community-level patterns of species distribution do not necessarily reflect uniform physiological responses. Instead, community structure along the Samin River appears to emerge from the differential ability of individual species to modulate stomatal traits in response to environmental heterogeneity.

Species with limited stomatal plasticity are likely constrained to specific sections of the river, whereas species with higher plasticity, such as *X. sagittifolium*, can persist across the full gradient.

Importantly, this species-specific interpretation also provides a clear rationale for the analytical focus on *X. sagittifolium* in quantitative statistical tests. Because it is the only species present across all gradients, it serves as a biologically appropriate model for assessing adaptive stomatal responses without conflating species turnover effects. This approach avoids overgeneralization and ensures that observed statistical patterns reflect true adaptive responses rather than artifacts of community composition.

Overall, the contrast between species-specific stomatal responses and community-level distribution patterns underscores the importance of integrating anatomical plasticity with species ecology. In riparian Araceae, the capacity for stomatal adjustment at the cellular level appears to be a key determinant of ecological breadth and persistence along the river continuum, reinforcing the value of species-focused anatomical analysis within broader community contexts.

This study demonstrates clear adaptive responses of riparian Araceae to abiotic variation along the upstream, midstream, and downstream gradients of the Samin River. A total of six species of the family Araceae were recorded, with the highest Araceae presence species occurring in the upstream and midstream sections, while only *X. sagittifolium* was found in the downstream area, indicating strong environmental filtering along the river continuum. *X. sagittifolium*, which was present across all river gradients, exhibited high environmental tolerance and emerged as the most resilient species in the study area. Stomatal morpho-anatomical analyses revealed interspecific variation in stomatal position, stomatal type, guard cell shape, and number of subsidiary cells, reflecting species-specific anatomical characteristics. Quantitative analyses further showed that stomatal number and density increased from upstream to downstream, whereas stomatal size decreased toward downstream gradient, indicating a coordinated adaptive response to changing abiotic conditions along the riparian gradient. These findings confirm that stomatal traits are sensitive indicators of plant adaptive responses to environmental variation and highlight their relevance for understanding plant resilience and informing conservation of riparian ecosystems. The observed stomatal patterns describe spatial variation across the three surveyed riparian sites of the Samin River, classified in gradient. Broader generalization to the entire river continuum will require replicated sites within each segment.

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