

Ecological plasticity in mangroves: mechanisms, drivers, and implications for resilience under global change

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Mangroves are foundational species of tropical and subtropical coastlines, providing critical ecosystem services despite thriving in one of the most physiologically challenging environments on Earth. Their remarkable ability to persist across steep gradients of salinity, anoxia, temperature, and tidal inundation is largely attributable to ecological plasticity - the capacity of a genotype to alter its phenotype in response to environmental variation. This article synthesizes current knowledge on the mechanistic basis, expression, and ecological consequences of plasticity in mangrove trees. We examine plastic responses across multiple biological scales: morphological (e.g., prop root and pneumatophore development, leaf succulence), anatomical (e.g., xylem vessel modifications, aerenchyma formation), physiological (e.g., salt excretion, hydraulic regulation, C₄-like carbon concentrating mechanisms), and life-history (e.g., crypto vivipary, flexible reproductive timing). We discuss how plasticity is constrained by genetic, energetic, and phylogenetic factors, and present a conceptual model linking plasticity to population-level resilience. Finally, we address the critical question of whether the current pace of climate change and anthropogenic modification exceeds the adaptive plastic capacity of mangroves. We argue that ecological plasticity serves as a primary buffer against environmental variability, but that extreme or novel conditions (e.g., rapid sea-level rise, freshwater diversion) can exceed plastic limits, leading to ecosystem collapse. Conserving plastic potential requires maintaining genetic diversity, hydrological connectivity, and disturbance regimes that allow phenotypic expression.

Keywords: *phenotypic plasticity, halophyte, acclimation, climate resilience, salt tolerance, Rhizophora, Avicennia, coastal wetlands*

Introduction

Mangrove forests occupy the intertidal zone of 118 countries, covering approximately 13.8 million hectares (Friess et al., 2019). They face daily fluctuations in salinity (0–90 ppt), tidal submergence, temperature, and wave energy, alongside chronic stressors such as waterlogged, sulfidic, and nutrient-poor sediments (Tomlinson, 2016). Unlike mobile organisms that escape stress, mangroves must tolerate or acclimate to *in situ* conditions. This requirement has driven the evolution of striking phenotypic variation differences in form and function among genetically similar individuals growing in contrasting microhabitats (Ball, 1988; Krauss et al., 2008). Ecological plasticity, distinct from genetic adaptation or ontogenetic programming, refers to the environmentally induced change in an organism's phenotype that enhances fitness or performance in the prevailing condition (Schlichting, 1986; Miner et al., 2005; Sultan, 2000). In mangroves, plasticity is not merely a passive response but an active, regulated suite of mechanisms that optimize resource acquisition and stress resistance (Wang et al., 2011). However, the term is often used loosely. Here, we adopt a strict definition: reversible or persistent, non-heritable changes in traits expressed by a single genotype in response to an environmental cue, resulting in improved or maintained function. The central thesis of this review is that ecological plasticity is the first line of defense against environmental variability in mangroves (Ellison & Farnsworth, 2001). While

genetic adaptation operates over generations, plasticity operates within the lifespan of an individual critical for long-lived trees (decades to centuries) facing unpredictable changes (Lovelock & Ellison, 2007). Nevertheless, plasticity has limits, and distinguishing between adaptive plasticity, maladaptive responses, and passive stress-induced damage is essential for predicting mangrove resilience (Reef & Lovelock, 2015). This article aims to catalogue the major axes of plastic response in mangroves, review the underlying physiological and molecular mechanisms, analyze the ecological and evolutionary consequences, and discuss implications for conservation under global change.

Environmental drivers of plasticity

Plastic responses in mangroves are triggered by specific environmental gradients (Krauss et al., 2008; Feller et al., 2010). The most potent drivers include

Driver	Spatial/Temporal Variation	Key Plastic Traits Affected
Salinity	0–90 ppt; daily (low tide) to seasonal	Leaf succulence, salt gland density, stomatal conductance, osmolytes (proline, glycine betaine) (Ball, 1988; Parida & Jha, 2010)
Tidal inundation	Hours to days; elevation differences of cm	Pneumatophore height/length, root lenticel hypertrophy, stem hypertrophy (Tomlinson, 2016)
Nutrient availability	Patchy; upwelling vs. terrigenous inputs	Root/shoot ratio, leaf N/P content, chlorophyll concentration, branching intensity (McKee et al., 2002; Feller et al., 2010)
Light	Gap vs. understory; seasonal sun angle	Specific leaf area, leaf angle, canopy layering, anthocyanin accumulation (Ball & Farquhar, 1984)
Anoxia & sulfide	Waterlogged sediments; redox potential < -150 mV	Aerenchyma proportion (root and stem), radial oxygen loss (ROL) barrier formation (Colmer, 2003)

Mechanisms and manifestations of plasticity

Morphological Plasticity

Morphological plasticity is the most visible form (Tomlinson, 2016). In *Avicennia marina* (grey mangrove), trees in high-salinity, high-wind zones develop short, sclerophyllous leaves with dense trichomes, while conspecifics in low-salinity, sheltered zones produce larger, thinner leaves (Ball, 1988). This represents an adaptive trade-off: smaller leaves reduce transpirational water loss and salt load, but at the cost of reduced carbon gain (Reef & Lovelock, 2015). Pneumatophores (vertical roots in *Avicennia*, *Sonneratia*) exhibit remarkable plasticity: their height increases with mean tide level to maintain aerial contact (Tomlinson, 2016). In *Avicennia germinans*, pneumatophore density can increase fivefold in waterlogged vs. well-drained soils, enhancing oxygen uptake (McKee, 1995). Similarly, prop roots of *Rhizophora mangle* become more numerous and longer in soft, anoxic mud than in firm substrate, improving anchorage and aeration (Ellison & Farnsworth, 2001).

Anatomical plasticity

Xylem anatomy is highly plastic. Under high salinity, mangroves reduce vessel diameter and increase vessel frequency (vessel grouping), a configuration that reduces embolism risk under high transpirational tension (Sobrado, 2007). *Laguncularia racemosa* develops thicker cuticles and hypodermal water storage tissue when exposed to hypersaline conditions (Parida & Jha, 2010). Aerenchyma-spongy, gas-filled tissue is induced by hypoxia. In *Rhizophora*, secondary aerenchyma forms in the bark of submerged stems, a response reversible upon drainage (Colmer, 2003). Barrier layers to radial oxygen loss (ROL) form in roots exposed to stagnant, reduced sediments, restricting oxygen leakage from basal zones to allow deeper penetration into anoxic layers (Colmer, 2003).

Physiological plasticity

Physiological plasticity is rapid and reversible. Key mechanisms include,

Salt regulation: *Avicennia* actively excretes 40–60% of absorbed Na⁺ and Cl⁻ via salt glands on leaves; gland density doubles within 10 days of a salinity increase from 15 to 45 ppt (Ball, 1988). *Rhizophora* (non-excretor) instead uses ultrafiltration at roots and salt compartmentalization in vacuoles, with osmotic adjustment via accumulation of mannitol and proline (Parida & Jha, 2010; Wang et al., 2011).

Water use efficiency (WUE): Stable carbon isotope ratios ($\delta^{13}\text{C}$) indicate that mangroves shift from low to high intrinsic WUE under salinity or drought stress (Ball & Farquhar, 1984; McKee et al., 2002). Stomatal regulation is plastic: *Rhizophora stylosa* reduces stomatal conductance by 70% under high salinity but fully recovers when salinity declines (Reef & Lovelock, 2015).

Photosynthetic acclimation: Mangroves adjust light-harvesting antenna size and xanthophyll cycle activity under variable light. Shade-acclimated leaves show lower light compensation points and higher quantum yields (Ball & Farquhar, 1984).

Life-history plasticity

Mangroves display unique reproductive plasticity. Cryptovivipary (embryo germination within the fruit while still attached to the parent) is obligate in Rhizophoraceae, but the timing of propagule release is plastic: under high salinity or low light, propagules are retained longer, allowing additional biomass accumulation before dispersal (Tomlinson, 2016). *Bruguiera gymnorhiza* can delay propagule establishment for months, awaiting suitable salinity conditions (Duke et al., 1998). This plastic bet-hedging enhances recruitment success (Ellison & Farnsworth, 2001).

Costs and constraints on plasticity

Plasticity is not unlimited (cited in Miner et al., 2005). Several constraints apply:

Constraint Type	Description	Example in Mangroves
Energetic cost	Maintaining sensory, signaling, and response systems requires ATP (Sultan, 2000).	High salt gland density increases maintenance respiration by 15–25% in <i>A. marina</i> (Ball, 1988).
Reliability	Environmental cues may be unreliable (e.g., a brief rainfall event in a dry season).	Premature stomatal opening after a false cue can lead to embolism.
Genetic limits	Narrow genetic basis reduces reaction norm breadth.	Inbred <i>R. mangle</i> populations show 40% less plastic response to salinity than outbred ones (Krauss et al., 2008).
Phylogenetic conservatism	Clades differ in baseline plasticity.	Rhizophoraceae (e.g., <i>Rhizophora</i>) show less leaf morphological plasticity than Avicenniaceae (Duke et al., 1998).

Plasticity also has a temporal scale: short-term acclimation (hours to days) is largely physiological, whereas morphological remodeling (e.g., new root types) requires weeks to months (Tomlinson, 2016).

Plasticity and resilience: a conceptual model

We propose a hierarchical response model for mangroves facing environmental change (adapted from Lovelock & Ellison, 2007; Feller et al., 2010),

Physiological adjustment (seconds–days): Stomatal closure, osmotic adjustment, salt gland activation (Ball, 1988; Reef & Lovelock, 2015).

Morphological/acclimatory response (weeks–months): New leaf anatomy, root proliferation, branch reorientation (Tomlinson, 2016).

Population genetic adaptation (generations): Allele frequency change (e.g., in salt tolerance loci) (Schlichting, 1986).

Ecosystem state change (decades): If plastic limits are exceeded, mortality → community shift → habitat loss (Gilman et al., 2008).

Plasticity provides resilience only within a certain environmental envelope. Beyond that, mortality occurs. For example, *A. germinans* can acclimate to salinities up to 65 ppt via plasticity, but beyond 80 ppt, all individuals die regardless of prior acclimation an absolute physiological limit (Wang et al., 2011).

Global change and the limits of plasticity

Anthropogenic drivers are challenging plastic capacity (Gilman et al., 2008; Lovelock et al., 2015)

Sea-level rise (SLR): While mangroves can build elevation via root accretion (plastic root production), the current SLR rate (3–6 mm yr⁻¹ in many regions) exceeds the maximum vertical accretion rate of ~2 mm yr⁻¹ in carbonate-poor settings (Lovelock et al., 2015). Plastic root responses become ineffective.

Freshwater diversion and hypersalinity: Dams reduce river flow, increasing dry-season salinity >70 ppt. Even *Avicennia*'s salt excretion fails, leading to leaf burn and crown dieback (Duke et al., 1998; Gilman et al., 2008).

Novel stressors: Microplastic contamination, herbicides, and warming-driven pests (e.g., *Acanthococcus* scale insects) trigger maladaptive plastic responses (e.g., excessive ethylene production causing leaf abscission) (Feller et al., 2010).

The interaction of stressors is critical: high temperature reduces the efficacy of osmotic adjustment, narrowing the plastic range (Parida & Jha, 2010).

Conservation implications

Preserving ecological plasticity requires (Feller et al., 2010; Lovelock et al., 2015),

Maintaining environmental heterogeneity: Monoculture plantations reduce selective pressures for plastic genotypes. Natural tidal gradients must be preserved (Ellison & Farnsworth, 2001).

Genetic connectivity: Fragmented populations lose the standing genetic variation that underlies broad reaction norms. Translocations between contrasting salinity regimes may restore plastic potential (Krauss et al., 2008).

Reducing chronic stress: Nutrient pollution can reduce investment in stress-induced plasticity (e.g., fewer salt glands when nitrogen is high) (McKee et al., 2002).

Assisted acclimation: Experimental priming exposing seedlings to mild stress before out planting can enhance subsequent plastic capacity (Reef & Lovelock, 2015).

Conclusions

Ecological plasticity is a cornerstone of mangrove success in dynamic environments, operating via integrated morphological, anatomical, physiological, and life-history adjustments (Schlichting, 1986; Miner et al., 2005; Sultan, 2000). However, plasticity is not a panacea. The rapid pace of global change, particularly accelerating sea-level rise and hydrological alteration, may overwhelm even the remarkable plastic capacities of mangroves (Lovelock et al., 2015; Gilman et al., 2008).

Future research priorities include,

- Quantifying the heritability of plastic responses (reaction norm genetic variance) (Schlichting, 1986).
- Identifying epigenetic mechanisms (DNA methylation, histone modification) underlying reversible acclimation.
- Developing dynamic vegetation models that incorporate plastic responses, not just static tolerances (Feller et al., 2010).
- Field transplants across environmental gradients to measure real-time plasticity under climate change (Krauss et al., 2008).

Mangroves exemplify the power of phenotypic flexibility in nature. Understanding the limits of that flexibility is essential for predicting and managing the future of coastal ecosystems.

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Karem Sasidhar has conceived this idea and written full article.

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