

Salinity shifts trait-mediated photosynthetic response to flooding in salt-sensitive mangrove under sea-level rise

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Abstract

Background and Aims

With accelerating sea-level rise, estuarine mangrove are increasingly exposed to combined stresses of prolonged flooding and elevated salinity. Although flooding duration (FD) and salinity are widely recognized as key constraints, how they interact to influence photosynthetic capacity through trait-based mechanisms remains unclear.

Methods

We established an *in situ* mesocosm experiment with *Acanthus ilicifolius*, a salt-sensitive mangrove species, in both oligohaline (OSZ) and mesohaline salinity zones (MSZ) of an estuary. We measured photosynthetic gas-exchange and leaf structural traits across a broad FD gradient (0.3 to 16.1 h·d⁻¹) to assess variations in net photosynthetic rate (Pn) and its potential drivers.

Results

Pn exhibited a nonlinear (hump-shaped) response to FD, while elevated salinity suppressed this response and shortened the optimal FD. In OSZ, Pn varied independently of specific leaf area (SLA), leaf thickness (LT) and leaf dry matter content (LDMC), but was primarily constrained by stomatal conductance (Gs) via its regulation of intercellular CO₂ concentration (Ci), as indicated by positive coordination between Pn and both Gs and Ci. However, Pn showed positive coordination with LT and LDMC in MSZ, but decreased with increasing SLA and Ci, contrary to the predictions of the leaf economics spectrum.

Conclusions

While mangrove can maintain photosynthesis through stomatal adjustment under prolonged flooding, elevated salinity disrupts this regulatory mechanism, triggering a shift from stomatal to non-stomatal limitations associated with altered leaf structure. These findings provide a trait-based mechanistic explanation for the physiological vulnerability of mangrove regeneration under sea-level rise.

Introduction

Mangroves are valuable coastal ecosystems that are threatened by sea-level rise (SLR) (Gilman et al. 2008; Madhavan et al. 2024; Saintilan et al. 2020). SLR directly prolongs flooding duration (Li et al., 2020; Krauss et al. 2014), and furthermore drives seawater intrusion, causing elevated salinity (Kirwan et al. 2024). Under SLR scenarios, flooding and salinity stress are expected to interact synergistically, further threatening mangroves (Krauss et al. 2014; Saintilan et al. 2020). Photosynthesis is a core physiological process underlying plant carbon gain, playing a pivotal role in plant growth and survival (Ashraf and Harris 2013; Hussain et al. 2021). Therefore, understanding ecophysiological mechanisms, in which flooding and salinity interact to determine photosynthetic performance, is essential for predicting mangrove resilience under future climate scenarios.

Leaf traits explain how environmental factors constrain photosynthesis, providing critical insights into the ecophysiological mechanisms of photosynthesis under climate change (Niinemets, 2023; Onoda et al. 2017; Shipley et al. 2006). Net photosynthetic rate (P_n) directly represents the plant's photosynthetic capacity, while stomatal conductance (G_s) regulates CO_2 uptake and directly affects photosynthesis (Harrison et al. 2020). A positive correlation between P_n and intercellular CO_2 concentration (C_i) typically indicates that photosynthesis is primarily regulated by stomatal conductance. In contrast, when P_n increases and C_i decreases, non-stomatal limitations are implicated, which might be driven by leaf structure (Hutmacher and Krieg 1983; Yan et al. 2007). Leaf structural traits indirectly affect photosynthesis via constraints on CO_2 diffusion and resource allocation, and follow the leaf economics spectrum which describes the coordination photosynthetic and structural tissues (Wright et al. 2004). Leaves with a large specific leaf area (SLA) optimize light capture and minimize diffusive resistance. In contrast, high leaf dry matter content (LDMC) and leaf thickness (LT) are associated with greater physical resilience, but at the cost of reduced gas diffusion and lower resource allocation to photosynthesis (Niinemets et al. 1999; Onoda et al. 2017). Therefore, examining the coordination between P_n and associated leaf traits under flooding and salinity stress can advance our understanding of photosynthetic regulation in mangroves under SLR (Niinemets et al. 2015; Yamori 2016).

Previous studies have shown that prolonged flooding duration and elevated salinity synergistically impairs photosynthetic capacity (Hussain et al. 2021; Madhavan et al. 2024; Krauss et al. 2006). Moderate flooding (e.g., $\leq 4 \text{ h d}^{-1}$) typically enhances CO_2 supply via increased stomatal conductance and intercellular CO_2 exchange, and reduces diffusive resistance (higher SLA, lower LDMC and LT), thereby enhancing photosynthetic capacity (Chen et al. 2005; Poorter et al. 2009; Voesenek and Bailey-Serres 2015). Yet prolonged flooding ($> 4 \text{ h d}^{-1}$) constrains photosynthesis by restricting gas exchange, reducing light availability, and inducing root hypoxia (Ashraf and Harris 2013; Li et al. 2020; Voesenek and Bailey-Serres 2015). Conversely, salinity stress induces osmotic and ionic toxicity that directly impairs leaf anatomical structure, reducing mesophyll conductance, and inhibiting rubisco activity, thereby compromising the maintenance of photosynthesis (Ashraf and Harris 2013; Madhavan et al. 2024; Zahra et al. 2022). Concomitantly, it induces an increase in LT and LDMC (with a decrease in SLA), reflecting a conservative strategy characterized by enhanced leaf mechanical strength and durability at the expense of reduced CO_2 diffusion and photosynthetic resource investment (Meera et al. 2023; Poorter et al. 2009). Moreover, elevated salinity lowers soil water potential, thereby exacerbating osmotic stress under short flooding and compounding hypoxia-induced water uptake limitations under prolonged flooding (Flowers and Colmer 2008). Therefore, salinity stress intensifies flooding-induced suppression of photosynthesis and may even alter its underlying mechanism (via stomatal or non-stomatal limitations) (Wang et al. 2022).

Although plants maintain photosynthesis by dynamically coordinating it with associated leaf traits in response to environmental fluctuations (Niinemets et al. 2015; Niinemets 2023; Yamori 2016), this coordination can be disrupted under increasing environmental stress, indicating a shift in the regulatory photosynthetic process from these factors (Bryant et al. 2024; Xing et al. 2021; Zandalinas et al. 2022). For example, as the water-table depth level decreased, the slope of SLA- P_n also decreased (Wright and

Sutton-Grier 2012). Similarly, salinity stress inverted a positive Pn-Ci correlation to negative, revealing non-stomatal limitations on photosynthesis (Yan et al. 2007). This change in the relationship between photosynthesis and associated leaf traits indicates a fundamental shift in environmental control, forcing a trade-off between growth and survival (Langley et al. 2022). While numerous studies have documented how mangroves respond to single stressors (flooding or salinity) (Cao et al. 2023; Chen and Wang 2017; Li et al. 2020; Negrão-Rodrigues et al. 2025; Wang et al. 2022), the coordination of photosynthesis and associated leaf traits under combined stressors remains poorly quantified.

While mangroves are typically regarded as salt-tolerant, different species vary significantly in their salinity tolerance, and salt-sensitive species may be most vulnerable under SLR (Perri et al. 2023; Wang et al. 2022; Ye et al. 2005). Compared to salt-tolerant mangrove species (such as *Avicennia* spp) with broad distributions across salinity zones, salt-sensitive mangrove species such as *Acanthus ilicifolius* and *Heritiera littoralis* are limited to oligohaline salinity zones (0.5 ~ 6 PSU) (Bryant et al. 2024; Ye et al. 2005; Zhang et al. 2012). *A. ilicifolius*, widely distributed in eastern and southeast Asia and northern Australia, exhibits high tolerance to flooding but low tolerance to salinity with growth significantly inhibited at salinity exceeding 15 PSU (Bryant et al. 2024; Tomlinson, 2016; Ye et al. 2005). Due to its broad distributions across tidal elevations, it represents an ideal model species for investigating interaction of flooding and salinity. Given these vulnerabilities, a study of *A. ilicifolius* is critical for detecting early photosynthesis-induced ecophysiological mechanisms caused by flooding and salinity, to avoid overestimating mangrove resilience under accelerating SLR.

In this study, we specifically implemented an *in situ* mesocosm experiment across two salinity zones to simulate SLR, representing the core (optimal) and marginal (stressful) habitats of *A. ilicifolius*. This study addresses two key scientific questions: (1) How does salinity stress alter the response and coordination of photosynthesis and associated leaf traits of salt-sensitive mangroves along a flooding gradient? (2) Does salinity stress alter trait-mediated regulation mechanisms of photosynthesis along a flooding gradient? By quantifying how flooding and salinity interact to affect photosynthetic capacity, associated leaf traits, and their coordination, this study aims to advance the mechanistic understanding of salt-sensitive mangrove resilience under accelerating SLR.

Materials and methods

Study area and species

Our study was conducted in the Zhangjiang Estuary Mangrove National Nature Reserve (23°55'N, 117°28'E), Fujian Province, China (Fig. 1a). Located north of the Tropic of Cancer, this site hosts one of the most extensive and structurally intact mangrove ecosystems in China. Over the past five years (2018 ~ 2022), the site has experienced an annual mean temperature of 22.9 °C, with the highest monthly mean temperature in August and the lowest in January. Annual precipitation averaged 1219 mm, predominantly occurring between April and September. The estuary experiences a semidiurnal tide, with a mean tidal range of 2.32 m and a maximum of 4.67 m. Driven by the interplay of tidal flooding and

freshwater discharge, a natural salinity gradient is established along the estuary. Following Zhang et al. (2012) and Wang et al. (2025), the estuary can be divided into oligohaline (0 ~ 6 PSU), mesohaline (13 ~ 18 PSU), and polyhaline (21 ~ 26 PSU) zones, each dominated by mangrove species with distinctive salt tolerances. Field surveys along the Zhangjiang estuary showed that, *A. ilicifolius* is primarily distributed in the upstream oligohaline zone, less frequently in the midstream mesohaline zone, and absent from the downstream polyhaline zone. In the oligohaline zone, *A. ilicifolius* exhibits a broad vertical distribution (spanning ~ 125 cm in elevation), where it forms a dominant component of the mangrove vegetation. In the mesohaline zone, *A. ilicifolius* occurs mainly as scattered tufts across intertidal zones.

In situ mesocosm experimental design

To simulate the impact of a SLR-induced salinity increase, we selected two salinity zones along the Zhangjiang Estuary: the oligohaline salinity zone (OSZ) (23°56'36.7"N, 117°22'42.5"E) and the mesohaline salinity zone (MSZ) (23°54'59.5"N, 117°25'46.9"E), representing the core and marginal distribution areas of *A. ilicifolius*, respectively (Fig. 1a). The two salinity zones are approximately 7 kilometers apart. To simulate the impact of a prolonged SLR-induced flooding duration, *in situ* mesocosm arrays were established in the OSZ and MSZ, following a 'marsh organ' design (Morris, 2007; Peng et al. 2018). The natural mudflat slope declines northward so the arrays were built sloping down toward the south to ensure the lower plants were not shaded by the upper ones. Each array was installed within tidal creeks at each salinity zone, spanning an elevation range of 225 cm (-50 ~ 175 cm above sea level, a.s.l.), with 0 cm defined as the lower elevational limit of *A. ilicifolius* (Fig. 1b). This gradient encompassed the species' natural elevational distribution (0 ~ 125 cm), extended below to simulate a prolonged flooding duration (-50 ~ -25 cm a.s.l.), and above to represent areas currently inaccessible due to coastal seawalls (150 ~ 175 cm a.s.l.). Each array contained 60 mesocosms arranged into 10 rows, with each row separated by 25 cm in elevation (Fig. 1b). Each row contained 6 mesocosms for plant cultivation (Fig. 1c). Each mesocosm was constructed from a 16-centimeter-diameter (200 cm²) PVC pipe, with the bottom 25 cm buried into the soil to facilitate water exchange between the mesocosm and the surrounding mudflat. All mesocosms were filled with sediment collected from adjacent mudflats for plant cultivation.

Plant cultivation

Ten *A. ilicifolius* propagules were planted in each mesocosm in July 2023, immediately after collection from naturally thriving populations in the OSZ of the Zhangjiang Estuary. To minimize intraspecific competition, seedlings were thinned one month after germination, following the emergence of true leaves, with only one individual retained per mesocosm. The beginning of the 2024 growing season (March) represented a critical period when the salinity differences between the two salinity zones were most pronounced, following prolonged exposure to high salinity during dry season in winter (Figure S1). At this stage, seedlings in the MSZ survived only within the elevational range corresponding to the species' natural distribution in the Zhangjiang Estuary. This indicates that our experimental setup

effectively captures *A. ilicifolius*'s ecologically relevant performance under field conditions, thereby justifying subsequent trait measurements as representative of its natural adaptive responses. At the time of sampling, surviving seedlings in the OSZ bore 12 ~ 26 fully expanded leaves and had a plant height of 13 ~ 47 cm, whereas those in the MSZ had 10 ~ 22 leaves and a plant height of 12 ~ 34 cm (measurement methods detailed in Appendix S1). Overall, 53 and 25 seedlings survived in the OSZ and MSZ, with 3–6 replicates per elevation treatment, except at -25 cm (n = 1) and 125 cm (n = 2) in the MSZ.

Leaf trait measurements

Leaf trait measurements were conducted on mangrove plants in March 2024, after eight months of exposure to experimental treatments. A mature, healthy leaf was selected from the second or third node below the apical bud of each surviving seedling (Table 1). Net photosynthetic rate (Pn), stomatal conductance (Gs), and intercellular CO₂ concentration (Ci) were measured *in situ* during low tide between 9:00 and 11:00 using a LI-6800 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) under optimal chamber conditions (see Appendix S1 for details). Following gas-exchange measurements, the same leaves were harvested, placed in ice-cooled containers, and transported to the laboratory for leaf thickness (LT), specific leaf area (SLA), and leaf dry matter content (LDMC) measurements (Pérez-Harguindeguy et al. 2016). Detailed measurement protocols are provided in the Supporting Information (Appendix S1).

Table 1
The abbreviations, units, implications and leaf traits referred to in this study.

Leaf traits	Abbreviations	Units	Implications	References
Net photosynthetic rate	Pn	$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Indicating photosynthetic capacity	(Hussain et al. 2021; Yamori 2016)
Stomatal conductance	Gs	$\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Controlling CO ₂ uptake for photosynthesis and water loss through transpiration	(Harrison et al. 2020)
Intercellular CO ₂ concentration	Ci	$\mu\text{mol}\cdot\text{mol}^{-1}$	Determining stomata and non-stomata limitations affecting photosynthesis	(Hutmacher and Krieg 1983; Yan et al. 2007)
Specific leaf area	SLA	$\text{cm}^2\cdot\text{g}^{-1}$	Indicating biomass cost of leaf construction per unit area and predicting adaption strategies	(Xing et al. 2021)
Leaf thickness	LT	mm	Effect on leaf defense and toughness as well as turnover rate	(Poorter et al. 2009)
Leaf dry matter content	LDMC	$\text{g}\cdot\text{g}^{-1}$	Indicating leaf resistance to physical hazards and plant strategies	(Poorter et al. 2009)

Environmental factor measurements

Environmental factors, mainly including seawater salinity and flooding duration, were systematically monitored, spanning from propagules plantation to leaf trait measurements (July 2023 to March 2024). In each zone, a conductivity/salinity data logger (HOBO U24-002-C, Onset, USA) was deployed at -50 cm to record seawater salinity every 10 minutes, and monthly averages were calculated. Water level was measured by deploying a pressure transducer (HOBO U20L-04, Onset, USA) at -50 cm as a proxy for water level and a second transducer was set above the high tide level to measure barometric pressure. Date, time, and pressure were recorded at 10-minute intervals during the course of the experiment, allowing for barometric pressure adjustments and calculation of the period of time that each elevation treatment was flooded. In addition, we measured porewater salinity and soil water content every month during the course of the experiment, with seven sampling times and three replicates per elevation (total $n = 21$), following the methods of Pennings and Richards (1998) (see Appendix S1 for details).

Seawater salinity ranged from 0.3 to 15.2 PSU (mean $\pm$ SE: 7.8 ± 2.1 PSU) in the OSZ and from 6.8 to 23.8 PSU (mean $\pm$ SE: 16.9 ± 2.2 PSU) in the MSZ during the experimental period (Fig. 1d). Flooding duration declined from 15.7 to 0.3 h/d with increasing elevation in the OSZ and from 16.1 to 0.3 h/d in the MSZ, and (Fig. 1e), reflecting slightly longer flooding in the MSZ due to tidal distortion caused by local estuarine geometry (Wang et al. 2025). Flooding duration directly and indirectly drives variations in soil porewater salinity (10.1 ~ 19.5 PSU in the OSZ; 21.7 ~ 35.1 PSU in the MSZ) and soil water content (43.8 ~ 26.5% in the OSZ; 51.4 ~ 26.6% in the MSZ), and other edaphic factors, all of which varied systematically with elevation (Figure S2). For instance, at higher elevations, shorter flooding duration (i.e., longer exposure time) leads to higher soil temperatures and greater evaporative loss, resulting in lower soil water content and elevated porewater salinity. This pattern aligns well with observed soil environmental gradients along natural tidal elevations in mangrove ecosystems (Da Cruz et al. 2013). Collectively, our experimental design effectively recapitulated the natural variation of flooding duration across tidal gradients in estuarine mangrove habitats.

Statistical analysis

Linear models were used to examine the effects of flooding duration, salinity zone and their interaction on photosynthetic capacity (P_n) and associated leaf traits (G_s , C_i , SLA, LT, LDMC). Leaf trait relationships were assessed using principal component analysis (PCA) in R using the vegan package (Dixon 2003). Additionally, Pearson's correlation coefficients among leaf traits were computed separately for each salinity zone. To further evaluate whether the coordination between P_n and associated leaf traits varied across salinity zones, we fitted additional linear models with P_n as the response variable and each associated leaf trait (G_s , C_i , SLA, LT, or LDMC) as a predictor, including salinity zone and its interaction with the predictor as fixed effects. Structural equation modeling (SEM) within each zone was conducted using the piecewise SEM package (Lefcheck 2016) to elucidate the pathways by which flooding duration influenced P_n through the regulation of associated leaf traits and the difference between two salinity zones. The SEM was constructed based on established physiological relationships (Table S1), with an a

priori path structure reflecting the mechanistic hypothesis that flooding duration affects Pn both directly and indirectly—via its effects on leaf structural traits (SLA, LT, LDMC) and stomata (Gs) (Figure S3). Model fit was evaluated using Fisher's C test and *P* value. All statistical analyses were conducted using R version 4.4.2.

Results

Response of leaf traits to flooding duration in the two salinity zones

Flooding duration (FD), salinity zone and their interaction had significant effects on leaf traits (Fig. 2 and Table 2). Pn and Gs exhibited a nonlinear (hump-shaped) response to increasing flooding duration in both salinity zones, but were significantly suppressed under salinity stress, with a significant FD × salinity zone interaction ($P < 0.001$). The optimal flooding duration for peak Pn shifted from 10.2 h/d in the OSZ to 4.8 h/d in the MSZ, accompanied by a 35.1% decline in peak Pn (from 13.4 to 8.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 2a). Gs exhibited a parallel response pattern to Pn (Fig. 2b). Ci and SLA increased with flooding duration, with a significantly steeper slope in the MSZ than in the OSZ (FD × salinity zone interaction, $P < 0.05$), such that MSZ plants exhibited lower trait values under short flooding (0 to 6 h/d) but surpassed OSZ plants under prolonged flooding (12 to 14 h/d) (Fig. 2c-d). LT and LDMC both decreased with increasing flooding duration, but only LT showed a significant FD × salinity zone interaction: its decline was markedly steeper in the MSZ ($P < 0.001$), whereas LDMC decreased at comparable rates in both zones ($P = 0.49$) (Fig. 2e-f).

Table 2

Linear models used to test the effects of flooding duration (FD or FD²) and salinity zone, including their interactions on leaf traits of *Acanthus ilicifolius*. *P*-value in bold indicates a statistically significantly result ($P < 0.05$).

Leaf traits	Factor effects	Df	F	P-value
New photosynthetic rate (Pn)	FD ²	2	37.92	< 0.0001
	Salinity zone	1	238.46	< 0.0001
	FD ² × Salinity zone	2	57.35	< 0.0001
Stomatal conductance (Gs)	FD ²	2	43.70	< 0.0001
	Salinity zone	1	141.84	< 0.0001
	FD ² × Salinity zone	2	21.56	< 0.0001
Intercellular carbon dioxide concentration (Ci)	FD	1	47.72	< 0.0001
	Salinity zone	1	2.74	0.1023
	FD × Salinity zone	1	35.25	< 0.0001
Specific leaf area (SLA)	FD	1	71.33	< 0.0001
	Salinity zone	1	5.00	0.0283
	FD × Salinity zone	1	6.93	0.0103
Leaf thickness (LT)	FD	1	27.53	< 0.0001
	Salinity zone	1	6.41	0.0135
	FD × Salinity zone	1	23.89	< 0.0001
Leaf dry matter content (LDMC)	FD	1	45.01	< 0.0001
	Salinity zone	1	0.13	0.7195
	FD × Salinity zone	1	0.48	0.4921

Relationships among leaf traits in the two salinity zones

Trait relationships differed markedly between OSZ and MSZ. In the OSZ, the first two principal components (PCA1 and PCA2) explained 48.9% and 28.3% of the total variation in leaf traits, respectively (Fig. 3a). Pn exhibited a positive correlation with Gs and Ci. SLA was negatively correlated with both LDMC and LT. However, no significant linear relationships were observed between SLA and Pn, Gs, or Ci, despite a positive trend (Fig. 3a and Table S2). In the MSZ, PCA1 explained 77.9% of the variance, showing that Pn and Gs were negatively correlated with Ci and SLA, but positively correlated with LDMC and LT (Fig. 3b and Table S2).

The strength or direction of the relationships between Pn and associated leaf traits varied across salinity zones, with significant leaf trait × salinity zone interactions. In both salinity zones, Pn increased with Gs, but the slope of the Gs-Pn relationship was significantly steeper in the MSZ than in the OSZ ($P < 0.001$) (Fig. 4a and Table 3). In the OSZ, Pn increased with Ci, but this relationship was reversed in the MSZ ($P < 0.001$) (Fig. 4b-c and Table 3). Pn was negatively but non-significantly correlated to SLA, LT and LDMC in the OSZ, whereas positive and significant relationships emerged in the MSZ ($P < 0.01$) (Fig. 4d-e and Table 3).

Table 3
Summary (parameter estimates) of linear models evaluating interactive effects of associated leaf traits (Gs, Ci, SLA, LT, LDMC) and salinity zone on photosynthetic capacity (Pn). *P*-value in bold indicates a statistically significantly result ($P < 0.05$).

Factor effects	Df	F	<i>P</i> -value
Gs	1	283.00	< 0.0001
Salinity zone	1	15.95	0.0002
Gs × Salinity zone	1	54.69	< 0.0001
Ci	1	17.61	< 0.0001
Salinity zone	1	74.17	< 0.0001
Ci × Salinity zone	1	44.63	< 0.0001
SLA	1	4.59	0.0355
Salinity zone	1	76.77	< 0.0001
SLA × Salinity zone	1	30.77	< 0.0001
LT	1	7.32	0.0085
Salinity zone	1	66.96	< 0.0001
LT × Salinity zone	1	9.77	0.0025
LDMC	1	0.30	0.5828
Salinity zone	1	65.11	< 0.0001
LDMC × Salinity zone	1	22.93	< 0.0001

Direct and indirect pathways affecting Pn

The structural equation model (SEM) revealed that flooding duration influenced Pn indirectly by modulating associated leaf traits, with contrasting pathways in the two salinity zones (Fig. 5). In the OSZ, flooding duration promoted Pn primarily by increasing Gs, while increasing SLA (due to reduced LT and

LDMC) negatively affected Gs (Fig. 5a). In contrast, in the MSZ, flooding duration no longer enhance Pn through Gs (e.g., it instead exerted a non-significant negative effect on Gs), but continued to reduce Pn through increased SLA (Fig. 5b). Compared to the OSZ, the standardized total effect of Gs on Pn decreased significantly in the MSZ (Fig. 5c-d). Conversely, the effects of SLA, LT, and LDMC on Pn increased in the MSZ. Overall, across the observed flooding gradient the net effect of flooding duration on Pn was positive in the OSZ but turned negative in the MSZ.

Discussion

Here, we established an *in situ* flooding gradient experiment at the core (OSZ) and marginal (MSZ) distribution areas for *A. ilicifolius*, where salinity stress in MSZ was found to limit its distribution. We found that salinity stress not only reshaped the responses of photosynthesis and associated leaf traits to flooding duration, but also altered their coordination and adaptive integration. More critically, our findings demonstrated that salinity stress fundamentally altered the mechanisms by which flooding controlled photosynthesis, specifically from stomatal limitations to non-stomatal limitations. Consequently, our study emphasizes the need to explicitly account for salinity stress when assessing mangrove adaptations to SLR-induced flooding, especially in salt-sensitive species. By elucidating the physiological and functional significance underlying leaf traits, this work provides critical mechanistic insights into photosynthesis in mangroves under SLR.

Salinity reshapes the response of photosynthesis and associated leaf traits along flooding gradients

In the OSZ, both short and long flooding durations inhibited the Pn of *A. ilicifolius*, with optimal Pn observed at an intermediate flooding duration of 10.2 h/d (Fig. 2a). Consistent with our findings, previous studies have demonstrated that flooding exerts a “low-promotion, high-inhibition” effect on mangrove photosynthesis, in accordance with the Law of Tolerance (Chen et al. 2005; Li et al. 2020; Wang et al. 2022). Poor photosynthetic capacity under shorter flooding durations is attributed to osmotic stress caused by insufficient water supply (Ashraf and Harris 2013; Peng et al. 2018). In contrast, longer flooding durations can lead to physiological drought, as prolonged root hypoxia disrupts root hydraulic conductivity and active water uptake, despite saturated soil conditions, ultimately constraining photosynthesis (Krauss et al. 2008; Madhavan et al. 2024).

To acclimatize to flooding stress, *A. ilicifolius* adjusted its leaf traits. Moderate flooding promoted stomatal opening and increased CO₂ concentration (Fig. 2b-c). Leaves subjected to higher flooding durations were thinner, with lower LDMC and higher SLA (Fig. 2d-f). These responses reflect a strategy to enhance gas exchange, light capture, and resource use efficiency under hypoxic and low-light conditions (Krauss et al. 2006; Wang et al. 2022).

However, this flooding-induced phenotypic plasticity was critically constrained by salinity. Importantly, our findings reveal that salinity stress significantly inhibited Pn across the entire flooding gradient, and

Pn declined sharply within the 8–16 h/d range (Fig. 2a). This interaction between flooding and salinity aligns with previous research (Chen and Wang 2017; Wang et al. 2022), which suggests that salinity reduces CO₂ supply through hydraulically induced stomatal closure and simultaneously damages the photosynthetic apparatus (Negrão-Rodrigues et al. 2025; Zahra et al. 2022). Notably, salinity stress reduced Gs and SLA, while increasing Ci and LT with a significant interaction between flooding and salinity (Fig. 2b-e). Similar salinity effects on leaf traits were also reported in previous studies (Cao et al. 2023; Meera et al. 2023). Salinity restricts water expenditure, disrupts cell structure, and necessitates increased resource allocation to defensive mechanisms to cope with intensified osmotic or anoxic stress (Cao et al. 2023; Krauss et al. 2008; Zahra et al. 2022). The underlying mechanism of flooding-salinity interactions may involve dual stress amplification: salinity stress exacerbates hypoxic stress under longer flooding duration while intensifying water deficit under shorter flooding duration (Flowers and Colmer 2008).

In previous studies on mangrove species with better salt-tolerance (such as *A. marina*), it was often found that a salinity level of 30 PSU or even higher would have an inhibitory effect on Pn and Gs (Wang et al. 2022; Yan et al. 2007). By contrast, the salt-sensitive *A. ilicifolius* experiences a severe reduction in photosynthetic capacity and associated leaf trait variations under combined flooding and salinity stress. Our results reveal the ecological basis for the predominance of salt-sensitive mangrove species in the OSZ (i.e. upstream in estuaries), and highlights their greater vulnerability compared to salt-tolerant species under SLR.

Salinity alters the coordination among photosynthesis and associated leaf traits along flooding gradients

In the OSZ, Pn increased with Gs and Ci (Fig. 4a-b), consistent with patterns observed in previous studies (Chen et al. 2005; Wang et al. 2022; Wang et al. 2023). The positive coordination among Gs, Ci and Pn indicates that stomatal regulation plays a key role in modulating carbon assimilation under flooding gradients (Hutmacher and Krieg 1983; Yan et al. 2007). We observed no significant coordination among Pn and leaf structure such as SLA, LT, and LDMC (Fig. 4c-e). High SLA facilitates greater light interception and faster gas diffusion, thereby supporting rapid photosynthesis (Voesenek and Bailey-Serres, 2015). Although not statistically significant, the direction of the relationships between Pn and structural traits in the OSZ aligns with leaf economics spectrum predictions (Fajardo and Siefert 2018; Jiao et al. 2016; Pan et al. 2020). This weak coordination likely reflects that, under flooding stress, photosynthetic capacity in *A. ilicifolius* is more strongly governed by dynamic stomatal regulation than by structural traits determined during leaf development (Wang et al. 2022).

However, this flooding-induced coordination was affected by elevated salinity. Previous studies have found the coordination between photosynthesis and associated leaf traits may shift under multiple environmental stressors (He et al. 2019; Wright and Sutton-Grier 2012; Xing et al. 2021). In the MSZ, the slopes of Pn-Gs increased (Fig. 4a), indicating that the increase or decrease in photosynthetic capacity is not entirely due to changes in stomata compared to OSZ. Moreover, the positive coordination between

Pn and Ci shifted to a negative correlation (Fig. 4b), providing additional evidence that non-stomatal factors are the primary constraints on photosynthesis (Ball and Farquhar 1984; Yan et al. 2007). The decline in photosynthesis is not primarily due to insufficient substrate supply from stomatal closure, but rather results from limitations in CO₂ diffusion to carboxylation sites (mesophyll conductance limitation) or damage to the photosystems and rubisco activity (biochemical limitations) (Li et al. 2020; Kozlowski 1997). Critically, our results showed that Pn decreased with increasing SLA and increased with higher LDMC and LT (Fig. 4c-e), a pattern reported along increasing light and temperature gradients, but contrary to the predictions of the leaf economics spectrum (Niinemets 2023; Puglielli et al. 2017; Wright et al. 2004). This might be because the thicker mesophyll performs similar functions to the epidermis, enhancing mechanical resistance while maintaining photosynthetic capacity (Niinemets 1999). The accumulation of photosynthetically competent tissues per unit area provides an explanation for the increases in Pn with increasing LT. The positive effects of increasing the photosynthetic tissue content are likely to more than offset the negative effects of intercellular transfer resistance increase (Niinemets 1999, 2023).

Overall, under multiple stressors, plants undergo adaptive strategy and photosynthetic regulation mechanism shifts. However, this study did not further distinguish between mesophyll conductance and biochemical limitations on photosynthesis, and the coordination of photosynthetic capacity and leaf physical resistance needs to be further clarified under flooding and salinity stresses (Pan et al. 2026). The classic leaf economics spectrum framework may not fully apply to plant individuals under severe environmental stress, as exemplified by *A. ilicifolius* in this study, which was subjected to the interaction of flooding and salinity.

Salinity shifts the process by which flooding controls photosynthesis through associated leaf traits

Numerous studies have employed structural equation modeling (SEM) and path analysis to elucidate the mechanisms underlying plant photosynthetic maintenance (He et al. 2019; Wang et al. 2023). In the OSZ, flooding duration enhanced photosynthetic capacity primarily by stimulating stomatal opening (Fig. 5a). The high standardized total effect of Gs on Pn, coupled with the positive indirect effect of flooding duration via Gs, indicates that flooding regulates photosynthesis predominantly through stomatal pathways (Fig. 5c). In contrast, this stomatal-mediated pathway was disrupted in the MSZ. Flooding exerted an indirect negative effect on photosynthesis by altering leaf structure traits (increasing SLA, and reducing LDMC and LT) (Fig. 5b, d). In the MSZ, the total effect of Gs on Pn decreased, whereas the influence of leaf structural traits increased (Fig. 5d). The physiological mechanism whereby flooding stimulates stomatal opening to enhance CO₂ assimilation is impaired under salinity stress, suggesting that the regulation of photosynthesis shifts under such conditions, potentially through stress-induced modifications in leaf structural (Niinemets 1999; Madhavan et al. 2024). This reversal may result from flooding-induced alterations in leaf structure under salinity stress, such as a reduction in mesophyll thickness, which ultimately diminishes photosynthetic capacity (Madhavan et al. 2024).

Differences in how flooding regulates photosynthesis across salinity regimes may control the distinct zonation patterns of salt-tolerant and salt-sensitive mangrove species (Bryant et al. 2024; Perri et al. 2023; Wang et al. 2022). Our results provide convincing evidence that salinity significantly alters the intrinsic mechanisms of flooding-controlled photosynthesis of *A. ilicifolius* under SLR. Taken together, these findings indicate that associated leaf traits mediate the effects of stressor on photosynthetic capacity; however, this mediation is modulated by changes in other stressors, highlighting the context-dependent nature of trait-function relationships under multiple stressors. This shift in photosynthetic regulation reduces carbon fixation in the MSZ under prolonged flooding, ultimately compressing the optimal habitat to salt-sensitive mangroves under accelerating SLR. We propose that future studies focus on other species to identify the salinity thresholds at which shifts in photosynthetic mechanisms occur, thereby enabling a more comprehensive understanding of mangrove community composition dynamics under SLR. Moreover, future studies should incorporate monitoring of soil physicochemical properties (e.g., soil temperature, pH, redox potential, and nutrient availability) across flooding gradients to elucidate how flooding indirectly modulates photosynthesis and leaf functional traits through alterations in the rhizosphere environment (Wang et al. 2023).

Conclusions

Based on an *in-situ* mesocosm experiment, we demonstrated that the Pn of *A. ilicifolius* exhibited a hump-shaped trend along the flooding gradient, and salinity stress led to a substantial decline in Pn, altering the coordination between Pn and photosynthetic-associated traits. While mangroves initially maintain photosynthesis via stomatal adjustment under flooding conditions, added salinity stress leads to reductions in leaf thickness and dry matter content, impairing mesophyll conductance and biochemical function—providing evidence of a shift from stomatal to non-stomatal limitations. We highlight that salinity fundamentally alters the trait-based ecophysiological mechanism by which flooding controls photosynthesis, leading to a sharp decline in photosynthetic capacity. Our results provide a mechanistic explanation for the physiological collapse of salt-sensitive mangrove species under accelerating SLR and identify this photosynthetic shift as an early warning signal of ecosystem vulnerability. Future studies should explore the relative contributions of mesophyll and biochemical limitations to photosynthetic decline under SLR, and link these physiological responses to individual growth and distribution patterns. Given their heightened vulnerability, salt-sensitive mangrove species deserve special attention, as understanding their photosynthetic plasticity and mechanistic shifts under SLR offers actionable pathways for conservation, restoration, and adaptive management.

Declarations

Conflict of interest

All authors declare that they have no conflict of interest.

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Author contributions

Dan Peng, and Yihui Zhang conceived of and designed this study. Muwen Niu, Yasong Chen, Lin Jin conducted the construction of marsh organs, seedlings cultivation and traits measurement. Muwen Niu and Yasong Chen analyzed the data, created the figures, and wrote the original manuscript. Karyne M. Rogers, Xin Song, Hao Wu, Dan Peng and Yihui Zhang reviewed and edited the manuscript. All authors reviewed the paper and approved the final manuscript.

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Data availability statement

The data supporting the results and the R scripts used to generate the analyses are available at the Dryad Digital Repository

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Figures

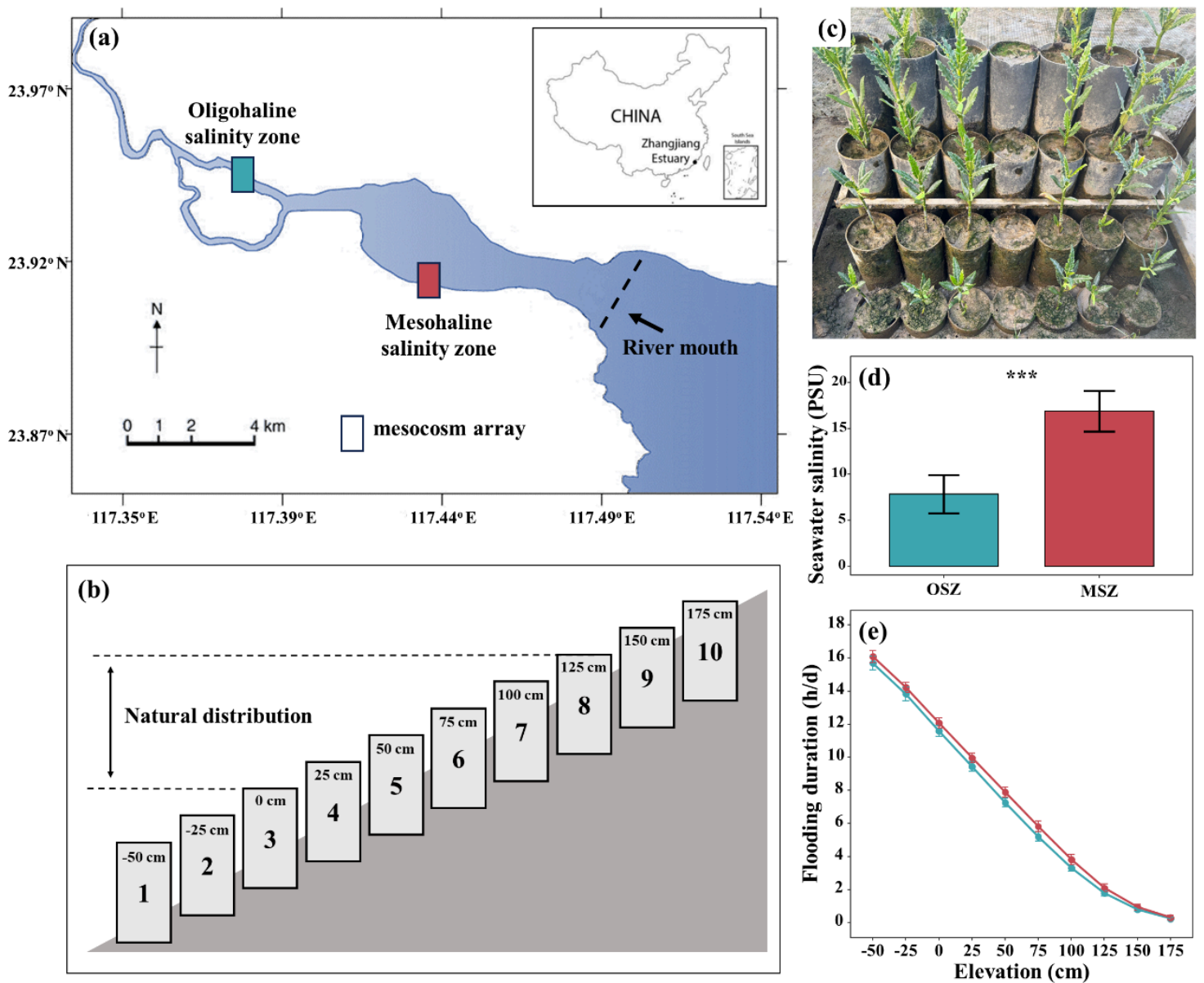


Figure 1

(a) Locations of the mesocosm array (rectangle) in Zhangjiang Estuary, Fujian Province, China. (b) Elevation setting diagram of mesocosm array. (c) Picture of mesocosm array and mangrove seedlings (the empty PVC tube was intentionally left unseeded to represent an uncolonized microsite). (d) Differences of seawater salinity in the two salinity zones, *t*-tests were performed to compare salinity changes between the two zones. (e) Variations of flooding duration across the tidal elevation in the two salinity zones

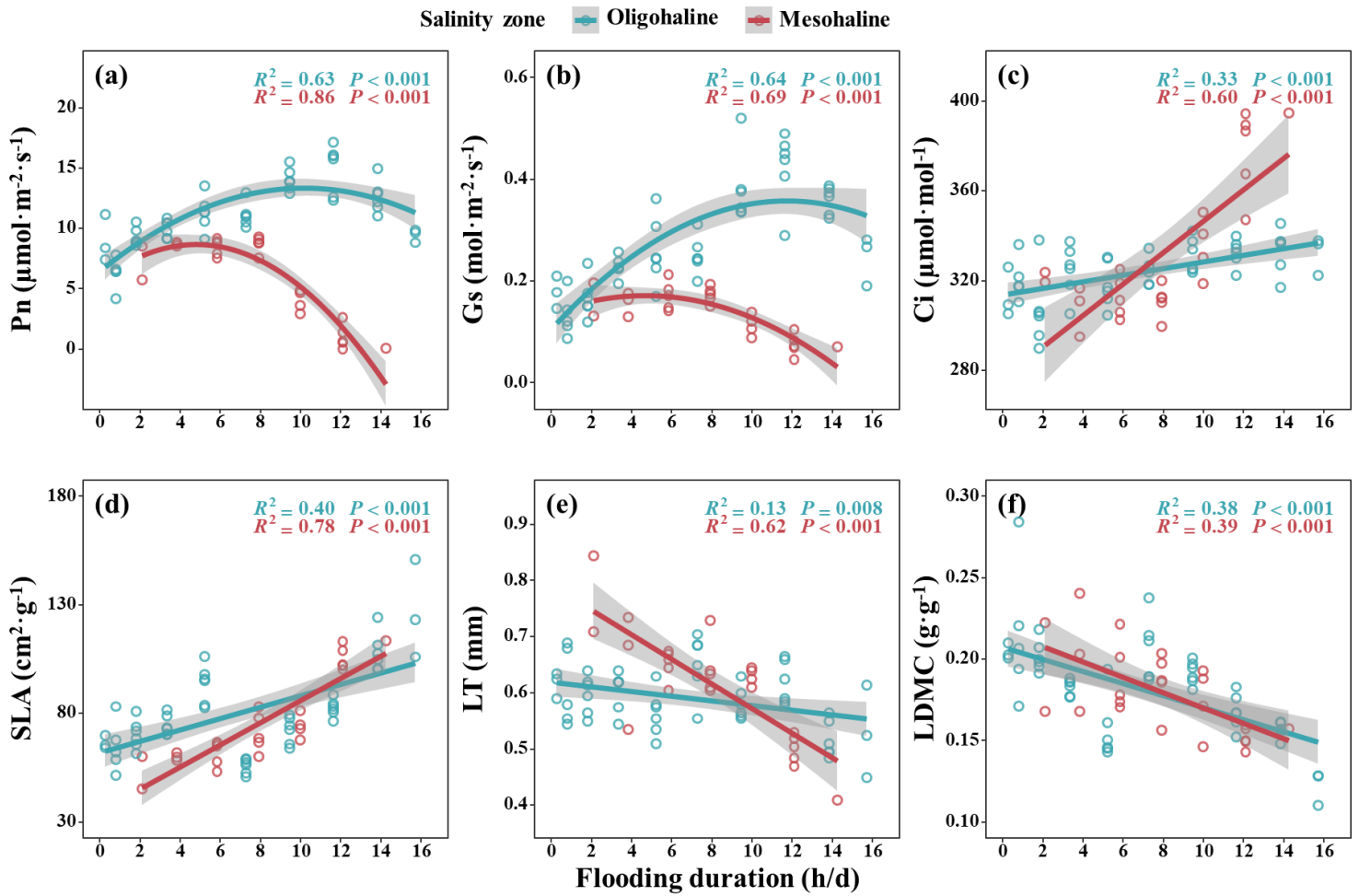


Figure 2

Leaf trait responses to flooding duration in *Acanthus ilicifolius* across oligohaline and mesohaline salinity zones. (a) Net photosynthetic rate, (b) Stomatal conductance, (c) Intercellular CO₂ concentration, (d) Specific leaf area, (e) Leaf thickness and (f) Leaf dry matter content. Shadow regions correspond to 95% confidence intervals. The legend of leaf traits is available in Table 1.

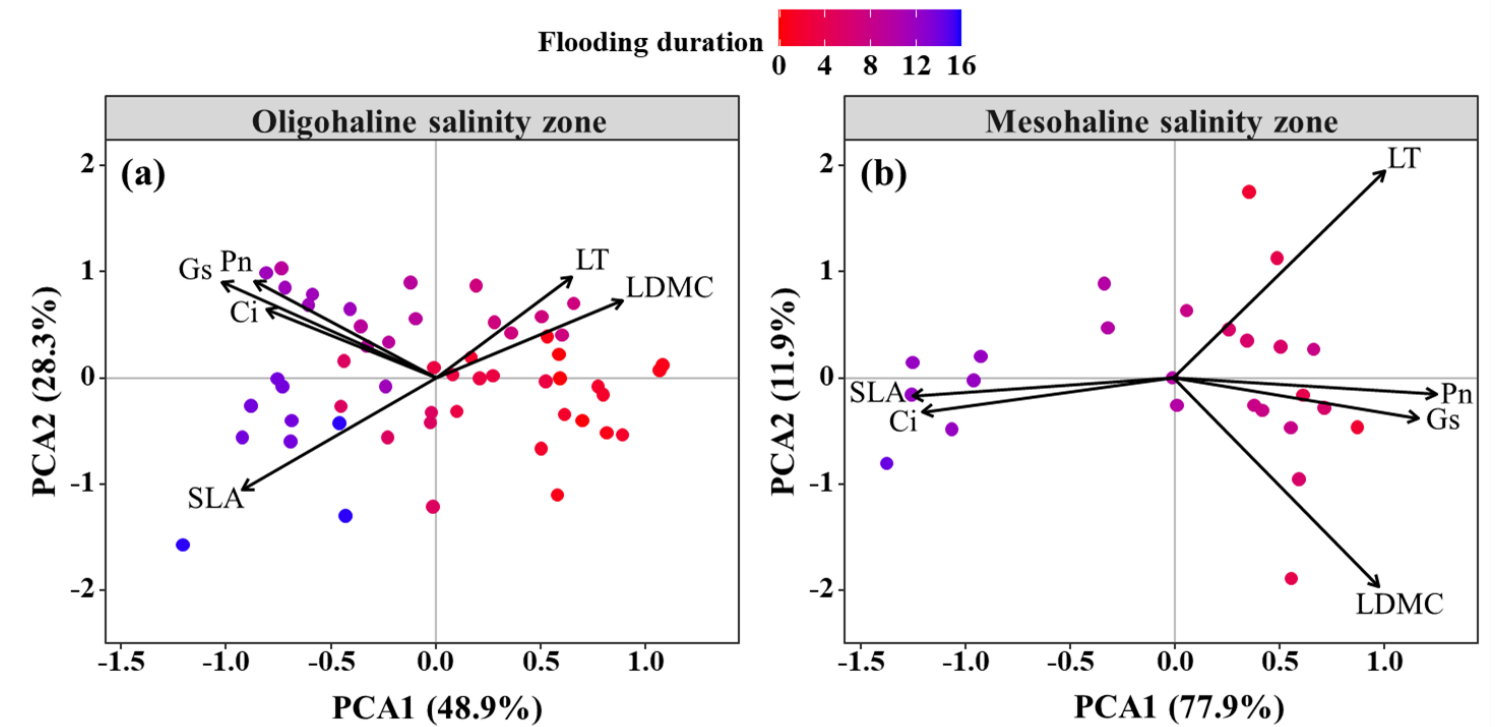


Figure 3

Principal component analysis (PCA) of *Acanthus ilicifolius* leaf traits in the (a) oligohaline and (b) mesohaline salinity zones. PCA plot color indicates the flooding duration, and blue to red gradient indicates the decrease in flooding duration. The legend of leaf traits is available in Table 1.

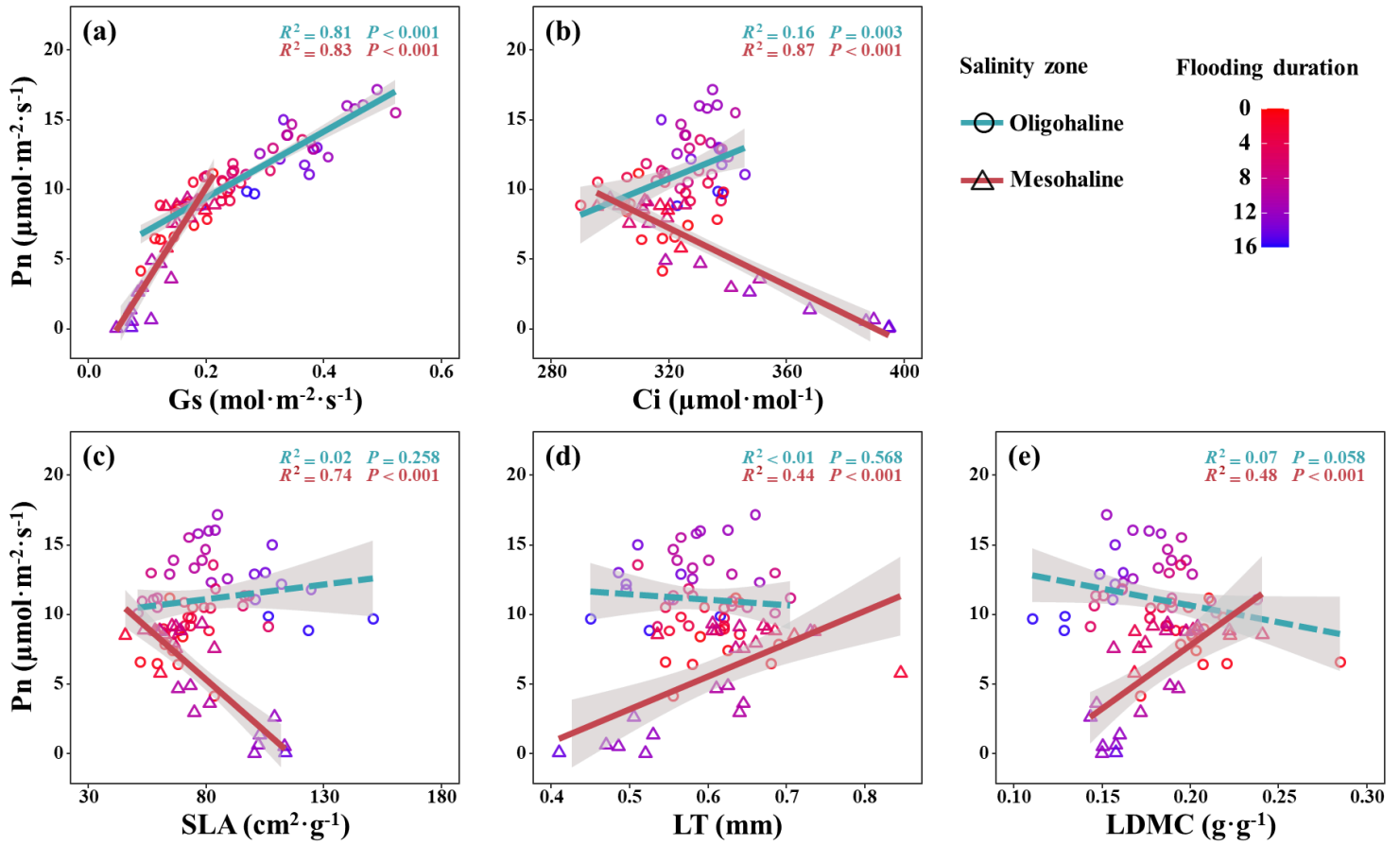


Figure 4

Relationship between the photosynthetic capacity and associated leaf traits of *Acanthus ilicifolius* in the oligohaline and mesohaline salinity zones. (a) Stomatal conductance, (b) Intercellular CO_2 concentration, (c) Specific leaf area, (d) Leaf thickness and (e) Leaf dry matter content. Point color indicates the flooding duration, and blue to red indicates the decrease in flooding duration. Shadow regions correspond to 95% confidence intervals. The legend of leaf traits is available in Table 1.

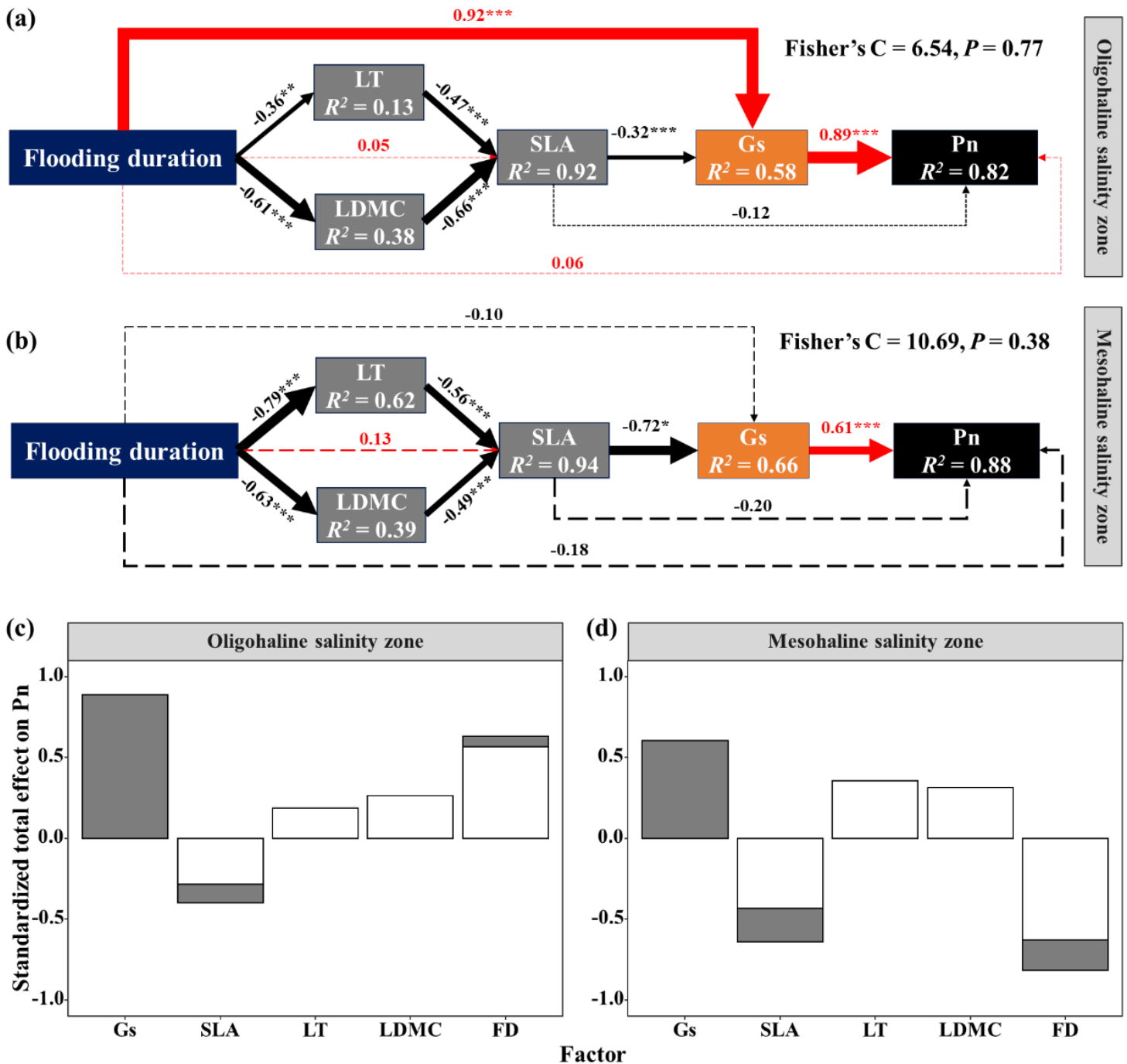


Figure 5

Structural equation models (SEM) illustrating the plausible effects of flooding duration and associated leaf traits on the photosynthetic capacity of *Acanthus ilicifolius* in (a) oligohaline and (b) mesohaline salinity zones. The standardized total effects (direct and indirect) from factors to Pn in the (c) oligohaline and (d) mesohaline salinity zones. Red and black arrows represent significant positive and negative pathways, respectively, and dashed arrows indicate insignificant pathways. The width of each significant path is proportional to its standardized path coefficient. The legend of leaf traits is available in Table 1. The standardized path coefficients and significance levels ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$) are shown beside the arrow of each path.

Supplementary Files

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