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Environmental Drivers of Regeneration in *Scyphiphora hydrophyllacea*: Thresholds for Seed Germination and Seedling Establishment in Hainan's Intertidal Zones

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Abstract

The endangered mangrove *Scyphiphora hydrophyllacea* is found in China only in Hainan's intertidal zones. Its populations are declining severely due to anthropogenic disturbances and regeneration failure. To clarify its environmental adaptation mechanisms, we investigated the effects of temperature, light intensity, photoperiod, salinity, soil, and flooding cycle on seed germination, seedling growth, and physiological traits, revealing that (1) the optimal germination conditions for seeds were 30–35 °C, 24 h continuous illumination at 25,000 lux, and 0‰ salinity, with soil type showing no significant effect ($p > 0.05$); (2) seedlings at 1–2 months post-germination achieve maximal growth at 30 °C in non-saline conditions, with salinity suppressing growth and light intensity affecting only crown expansion; and (3) flooding responses are age-dependent: seedlings at 1–2 months post-germination show optimal growth at 8 h per day (100% survival), while 12 h (h) per day reduces survival by 13.3%. One-year-old seedlings exhibit distinct strategies: 4 h per day flooding induces escape responses (peak growth, chlorophyll, sugars), 8 h per day shows photosynthetic compensation despite metabolic trade-offs, and 12 h per day triggers tolerance mechanisms (biomass maximization via structural reinforcement). These findings demonstrate *S. hydrophyllacea*'s multifactorial adaptation to intertidal conditions, providing critical physiological benchmarks for conservation strategies targeting this threatened ecosystem engineer.

Keywords: endangered mangrove; *Scyphiphora hydrophyllacea*; environmental factors; germination traits; seedling growth

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1. Introduction

Mangrove forests represent one of Earth's most productive wetland ecosystems, occupying approximately 170,000 km^2 across tropical and subtropical coastlines [1]. These unique intertidal communities play an irreplaceable role in carbon sequestration, shoreline stabilization, and biodiversity conservation [1]. Specifically, mangrove forests exhibit exceptional biogeochemical efficiency, with net primary productivity rates exceeding 2.5 kg C·m^{-2}·year^{-1} [2]. Functioning as coastal bioshields, mangroves attenuate 66%–90% of wave energy during storm surges while trapping 240 Mg of sediment per hectare annually [3]. Their belowground carbon storage capacity is three to five times greater than that of

terrestrial forests [4]. Moreover, this carbon sequestration occurs alongside critical habitat provisioning. The complex root systems nurture juvenile stages of 75% of commercially important fish species, while the canopy structures host specialized avian and invertebrate communities [5]. Consequently, the conservation of mangrove ecosystems emerges as both an ecological imperative and socioeconomic necessity for achieving long-term coastal sustainability.

Despite covering only 0.14% of the global mangrove area, China harbors 33% of mangrove plant species, with Hainan Island serving as a critical biodiversity hotspot [6]. However, over 40% of China's mangroves have been lost since the 1950s, primarily due to land reclamation and invasive species [7]. The endangered mangrove species *Scyphiphora hydrophyllacea* C. F. Gaertn., a monotypic mangrove in the Rubiaceae family, exemplifies this crisis: its distribution in China has contracted from multiple sites to two remnant populations in Sanya and Wenchang [8]. Our investigations revealed that *S. hydrophyllacea* seeds germinated en masse during October−November, developing cotyledons, but seedling mortality increased sharply in subsequent months, leading to inefficient natural recruitment.

Mangrove regeneration is regulated by heterogeneous habitat conditions, particularly through complex interactions of salinity, light, temperature, and tidal regimes [9]. As a critical environmental filter, salinity exerts species-specific controls on establishment success. While *Avicennia germinans* (L.) L. propagules can root across an exceptional 0−57‰ salinity range [10], most mangrove species exhibit much narrower physiological limits. For instance, *Ceriops tagal* (Perr.) C. B. Rob. seedlings show 100% mortality at 60‰ [11], and *Sonneratia ovata* Backer shows an exceptionally restricted germination range of only 0−2.5‰ [12]. Light and temperature further mediate regeneration niches. Photoinhibition suppresses *C. tagal* hypocotyl emergence [13], while thermal extremes constrain species like *Lumnitzera littorea* (Jack) Voigt, whose seeds only germinate at 25 ± 5 °C [14]. Tidal inundation generates critical trade-offs in mangroves: moderate flooding enhances pneumatophore development [15], whereas prolonged submergence reduces photosynthetic efficiency by 40%–60% in *Avicennia marina* (Forssk.) Vierh. [16]. Such threshold-dependent responses remain unquantified in the endangered *S. hydrophyllacea*, which exhibits regeneration failure despite mass germination—a knowledge gap demanding urgent resolution for effective conservation.

This study systematically analyzes the effects of temperature, salinity, light intensity, photoperiod, flooding regime, and soil substrate on critical developmental stages of *S. hydrophyllacea*, encompassing seed germination and early seedling growth (1–2 months post-germination). Furthermore, we quantitatively assess the physiological responses of one-year-old seedlings to flooding stress, including osmotic adjustment compounds, photosynthetic parameters, and biomass allocation patterns, aiming to elucidate their physio-ecological adaptation thresholds, optimize propagation techniques for this endangered species, and provide scientific foundations for both natural and artificial restoration of mangrove wetlands.

2. Materials and Methods

2.1. Seed Collection

The study was conducted from June to November 2024. Mature seeds of *S. hydrophyllacea* were collected from its primary natural habitat in the Qingmei Port Mangrove Nature Reserve (18.2197° N, 109.6150° E) in Sanya. Healthy seeds from the same maternal tree were selected, soaked in distilled water for 24 h, and then used for germination experiments.

2.2. Study Materials

For germination trials, seeds were sown in plastic containers ($20 \times 15 \times 7$ cm^3) filled with 450 g of sterilized growth substrate (see below). Each container had four drainage holes at the bottom and was placed on a tray to prevent waterlogging.

For seedling cultivation, healthy 1–2-month-old seedlings (with fully expanded cotyledons) were selected for experiments. The seedlings were planted into multi-cell plastic containers ($5 \times 5 \times 7$ cm^3 per cell; one drainage hole per cell), which were placed inside larger containers ($20 \times 15 \times 7$ cm^3). Additionally, healthy one-year-old seedlings grown from seeds collected in June 2023 under identical conditions were used for flooding experiments. These seedlings (7–10 cm tall, 4–6 true leaves) were individually potted in 6 cm-diameter grow bags. The soil substrate consisted of a 1:1 (v/v) mixture of river sand ($\geq$80% sand content) and commercial potting soil (Hebei, China). Prior to use, the substrate was sterilized with a 0.25% $KMnO_4$ solution for 48 h, rinsed with distilled water, and sun-dried for 72 h.

2.3. Experimental Design for Seed Germination

2.3.1. Temperature and Photoperiod

Three temperature gradients (25 °C, 30 °C, 35 °C) and three photoperiod cycles (24 h light/0 h dark, 12 h light/12 h dark, 0 h light/24 h dark) were tested. All treatments were maintained in climate chambers (MGC-250BP-2, Yiheng, Shanghai, China) at 25 °C, 12,000 lux, and a 1:1 (v/v) sand:potting soil mixture (hereafter S1P1). Each treatment consisted of 50 seeds with three replicates.

2.3.2. Salinity and Light Intensity

Since our field monitoring in the natural habitat of *S. hydrophyllacea* recorded a minimum seawater salinity of 0‰, we used 0‰ as the lowest salinity level in our study. Four salinity levels (0‰, 2‰, 5‰, 10‰) were tested in a controlled-environment greenhouse (25 °C, 25,000 lux, 12L/12D, S1P1). Artificial lighting was provided by daylight-simulating fluorescent lamps (Philips T8 36W/865, 6500 K). For light intensity, two levels were compared: 25,000 lux (greenhouse) and 12,000 lux (climate chamber), with other conditions identical (25 °C, 12L/12D, S1P1). Each treatment consisted of 50 seeds with three replicates.

2.3.3. Soil Substrate

Four substrate mixtures were evaluated: (1) S1P1; (2) pure sand; (3) a 2:1 (v/v) sand:potting soil mixture (hereafter S2P1); and (4) a 2:1 (v/v) sand:red soil mixture (S2R1). All substrates were tested in the greenhouse (25 °C, 25,000 lux, 12L/12D). Each treatment consisted of 50 seeds with three replicates.

2.4. Experimental Design for Seedling Growth

2.4.1. Temperature

Seedlings were exposed to 25 °C, 30 °C, or 35 °C in climate chambers (12,000 lux, 12L/12D, S1P1). Each treatment included five seedlings with three replicates.

2.4.2. Salinity

Four salinity treatments (0‰, 5‰, 10‰, 20‰) were applied in the greenhouse (25 °C, 25,000 lux, 12L/12D, S1P1). Salt solutions were maintained at 1 cm depth in containers, refreshed weekly, and monitored daily to ensure stable salinity. Each treatment included five seedlings with three replicates.

2.4.3. Light Intensity

Two light treatments were applied in the greenhouse. The low light treatment (6000 lux) was achieved using six-needle shade nets, while the control groups received full light (25,000 lux), with other conditions constant (25 °C, 12L/12D, S1P1). Each treatment included five seedlings with three replicates.

2.4.4. Flooding Regime

Four daily flooding durations (0 h, 4 h, 8 h, 12 h) were simulated using a dual-tank tidal system (an upper growth tank/container + a lower reservoir/container). The flooding depth was maintained at 1–2 cm above the substrate surface. Hoagland's nutrient solution and salt solution (5‰) were supplemented every 14 days. All treatments were maintained in a greenhouse (25 °C, 25,000 lux, 12L/12D, S1P1). Each treatment included five seedlings with three replicates.

2.5. Data Collection

2.5.1. Germination Statistics

Germination (defined as radicle emergence $\geq$ 2 mm) was recorded daily until no new germination occurred for 14 consecutive days.

The four parameters included in the calculation were germination percentage (GP), germination energy (GE), mean germination time (MGT), and germination lag (GL) [17]. These parameters were calculated as follows:

GL (d) is defined as the number of days from sowing to emergence of the first radicle. (1)

$$\mathrm{GP}(\%) = \frac{\text{total number of germinated seeds}}{\text{number of test seeds}} \times 100 \quad (2)$$

$$\mathrm{GE}(\%) = \frac{\text{number of seeds germinated within 80 days}}{\text{numbers of test seeds}} \times 100 \quad (3)$$

$$\mathrm{MGT} = \frac{\sum(n_i \times t_i)}{\sum n_i} \quad (4)$$

where n_i represents the number of seeds germinated on day i after sowing, and t_i denotes the number of days after sowing.

2.5.2. Seedling Growth and Physiology Statistics

For 1–2-month-old seedlings, height, crown width, and leaf count were measured biweekly with a precision of 0.01 cm. Root length and biomass (fresh/dry weight of roots, stems, leaves) were assessed post-harvest. For one-year-old seedlings, height, basal diameter, and leaf number were tracked biweekly. The net photosynthetic rate was measured using an LI-6800 at 10:00–11:30 a.m. on clear days before harvest. Chlorophyll and soluble sugars were quantified using microplate assays from Zike Biotechnology in Shenzhen, China.

2.6. Data Analysis

Statistical analyses were performed using IBM SPSS Statistics 20.0. Normally distributed data (Shapiro–Wilk, $p > 0.05$) were analyzed using a one-way ANOVA with an LSD test to assess the effects of temperature, salinity, photoperiod, soil, and flooding gradients on *S. hydrophyllacea* regeneration ($p < 0.05$). Nonparametric alternatives were used otherwise (Kruskal–Wallis test with Mann–Whitney U post hoc). Independent *t*-tests were employed to determine whether changes in light intensity were statistically significant ($p < 0.05$). Data visualization was created using OriginPro 2021.

3. Results

3.1. Effects of Environmental Factors on S. hydrophyllacea Seed Germination

3.1.1. Temperature Effects on Seed Germination

S. hydrophyllacea seeds exhibited temperature-dependent germination dynamics. Initial germination rates (0–60 days) were highest at 35 °C, though this pattern reversed in later stages (Figure 1A). Final germination percentage (GP) and energy (GE) showed no significant differences across temperatures (25–35 °C; $p > 0.05$, Table 1). However, both mean germination time (MGT) and germination lag (GL) decreased significantly with increasing temperature ($p < 0.05$, $n = 150$), with 25 °C showing prolonged GL compared to 30–35 °C. These suggest the optimal temperature range for germination was 30–35 °C.

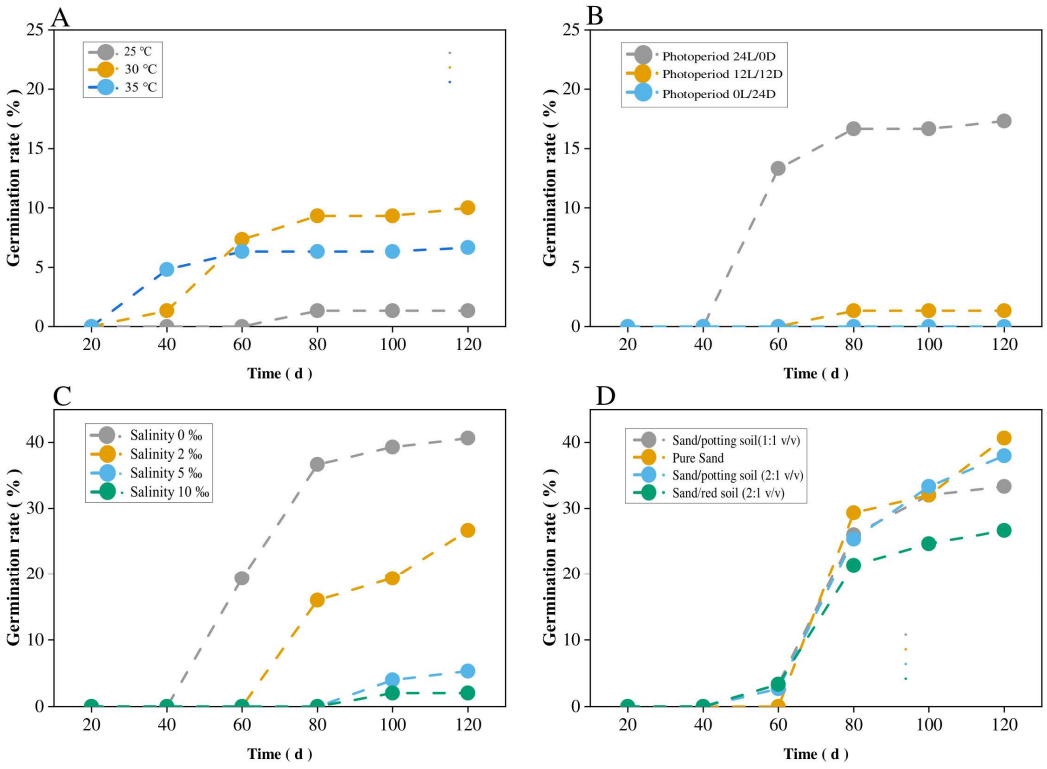


Figure 1. Temporal dynamics of germination rates of *S. hydrophyllacea* seeds under different environmental factors: (**A**) temperature; (**B**) photoperiod; (**C**) salinity; (**D**) soil substrate.

Table 1. Effects of environmental factors on seed germination parameters of *S. hydrophyllacea*.

Treatment		GE (%)	GP (%)	MGT (d)	GL (d)
Temperature	25 °C	1.33 ± 1.15 a	1.33 ± 1.15 a	77.00 ± 4.24 a	77.00 ± 4.24 a
	30 °C	9.33 ± 11.01 a	10.00 ± 10.58 a	57.01 ± 13.18 ab	45.00 ± 11.00 b
	35 °C	6.66 ± 6.11 a	6.66 ± 6.11 a	37.79 ± 0.76 b	33.00 ± 0.00 b
Photoperiod	24L/0D	16.66 ± 3.05 a	17.33 ± 3.05 a	57.11 ± 5.26 b	48.33 ± 1.15 b
	12L/12D	1.33 ± 1.15 b	1.33 ± 1.15 b	77.00 ± 4.24 a	77.00 ± 4.24 a
	0L/24D	-	-	-	-
Salinity	0‰	36.66 ± 1.15 a	40.67 ± 3.05 a	59.72 ± 7.71 b	50 ± 5.00 c
	2‰	36.66 ± 1.15 a	26.66 ± 5.77 b	85.40 ± 4.54 a	69.00 ± 0.00 b
	5‰	16.00 ± 6.00 b	5.33 ± 7.57 c	89.71 ± 5.25 a	90.00 ± 0.00 a
	10‰	0.00 ± 0.00 c	2.00 ± 2.00 c	97.25 ± 3.88 a	94.5 ± 7.77 a

Table 1. *Cont.*

Treatment		GE (%)	GP (%)	MGT (d)	GL (d)
Soil substrate	Sand/potting soil (1:1 *v*/*v*)	26.00 ± 2.00 a	33.33 ± 3.05 ab	74.40 ± 4.82 a	61.00 ± 6.00 a
	Pure Sand	29.33 ± 13.01 a	40.66 ± 6.11 a	80.50 ± 8.59 a	67.00 ± 0.00 a
	Sand/potting soil (2:1 *v*/*v*)	25.33 ± 8.08 a	38.00 ± 2.00 ab	78.13 ± 9.42 a	61.00 ± 6.00 a
	Sand/red soil (2:1 *v*/*v*)	26.67 ± 11.55 a	26.66 ± 11.54 b	71.03 ± 3.70 a	58.00 ± 3.00 a
Light intensity	12,000 lux	1.33 ± 1.15 b	1.33 ± 1.15 b	77.00 ± 4.24 a	77.00 ± 4.24 a
	25,000 lux	36.66 ± 1.15 a	40.67 ± 3.05 a	59.72 ± 7.71 b	50 ± 5.00 b

Note: GE: germination energy; GP: germination percentage; MGT: mean germination time; GL: germination lag; L/D: L = Light, D = Dark; *v*/*v*: volume by volume. Values are mean ± SD (n = 150). Different lowercase letters in the same column indicate significant differences at $p < 0.05$. '-' indicates no data.

3.1.2. Photoperiod Effects on Seed Germination

Photoperiod significantly influenced all germination parameters ($p < 0.05$, $n = 150$). Continuous illumination (24L/0D) yielded maximal GP (17%) and GE (17%), and showed significant advantages over other treatments (Table 1). The 24L/0D maintained significantly higher germination rates during days 40–80 ($p < 0.05$) than 12L/12D (Figure 1B). However, no germination occurred in complete darkness. These findings suggest that the seeds of *S. hydrophyllacea* exhibit positive photoperiod dependency.

3.1.3. Salinity Effects on Seed Germination

Germination exhibited strong salinity inhibition (Table 1). The 0‰ salinity achieved the highest GP (41%) and the shortest MGT (59.72 d), showing significant differences among treatment groups ($p < 0.05$, $n = 150$). This optimal freshwater response was further evidenced by (1) an 86.89%–95.08% reduction in germination at ≥5‰ salinity, and (2) consistently higher daily germination rates during days 40–80 (Figure 1C). These results identify freshwater conditions as critical for successful seed germination in *S. hydrophyllacea*.

3.1.4. Substrate Composition Effects on Seed Germination

The sandy substrate yielded the highest GP (40.66 ± 1.21%), which differed significantly from S2R2 (Table 1, Figure 1D). However, substrate type showed no significant effect on GE, MGT, or GL ($p > 0.05$, $n = 150$), indicating the seeds' broad adaptability to diverse soil substrates.

3.1.5. Light Intensity Effects on Seed Germination

As shown in Table 1, high light intensity (25,000 lux) maximized germination performance (GP: 40.67%; GE: 36.66%), representing 39.34% and 35.33% increases over 12,000 lux ($p < 0.05$, $n = 150$). These photoblastic responses confirm *S. hydrophyllacea* as a light-demanding species, with seed germination positively regulated by irradiance intensity.

3.2. Environmental Effects on S. hydrophyllacea Early Seedling Growth

3.2.1. Temperature Effects on Early Seedling Growth

S. hydrophyllacea seedlings exhibited a pronounced temperature-dependent growth ($p < 0.05$, $n = 15$, Table 2). The 30 °C treatment maximized height increment (Figure 2A) and leaf production, significantly outperforming 25 °C and 35 °C ($p < 0.05$). While root elongation at 25 °C (4.40 ± 1.79 cm) and 30 °C (4.65 ± 1.11 cm) were comparable, both exceeded 35 °C (2.16 ± 0.45 cm; $p < 0.05$). Notably, 35 °C induced a 73% mortality rate. Growth rate differentials between 30 °C and 25 °C became non-significant ($p > 0.05$) after

phase 3 (Figure 3A), though cumulative height at 30 °C remained superior throughout ($p < 0.05$). These results identify 30 °C as the optimal temperature for early seedling growth.

Table 2. Effects of environmental factors on seedling parameters of *S. hydrophyllacea*.

Treatment		Seedling Height Increment (cm)	Crown Expansion Increment (cm)	Number of Blades	Root Length (cm)	Mortality (%)
Temperature	25 °C	0.22 ± 0.07 b	0.33 ± 0.16 a	3.50 ± 1.44 b	4.40 ± 1.79 a	20
	30 °C	0.35 ± 0.10 a	0.45 ± 0.18 a	5.50 ± 1.87 a	4.65 ± 1.11 a	0
	35 °C	0.23 ± 0.09 b	0.35 ± 0.15 a	3.83 ± 0.57 b	2.16 ± 0.45 b	73.33
Salinity	0‰	0.32 ± 0.08 a	0.22 ± 0.08 a	3.86 ± 1.76 a	4.43 ± 1.08 a	0
	5‰	0.30 ± 0.07 a	0.29 ± 0.19 a	2.61 ± 0.96 a	3.39 ± 0.85 b	6
	10‰	0.16 ± 0.05 b	0.24 ± 0.13 a	2.75 ± 1.03 a	3.02 ± 0.72 b	46
	20‰	0.17 ± 0.08 b	0.19 ± 0.10 a	2.20 ± 0.63 b	3.09 ± 1.01 b	66
Light intensity	6000 lux	0.32 ± 0.08 a	0.22 ± 0.08 b	3.86 ± 1.76 a	4.43 ± 1.08 a	0
	25,000 lux	0.33 ± 0.10 a	0.36 ± 0.14 a	4.66 ± 1.79 a	4.16 ± 1.12 a	0
Flooding rhythm	0 h	0.32 ± 0.08 b	0.22 ± 0.08 b	3.86 ± 1.76 b	4.43 ± 1.08 a	0
	4 h	0.33 ± 0.09 b	0.28 ± 0.11 a	5.20 ± 1.01 a	4.50 ± 0.43 a	0
	8 h	0.38 ± 0.12 a	0.36 ± 0.17 a	4.53 ± 1.35 ab	4.41 ± 0.84 a	0
	12 h	0.41 ± 0.09 a	0.37 ± 0.14 a	4.84 ± 1.28 ab	4.73 ± 0.60 a	13.33

Note: Values are mean ± SD ($n = 15$). Different lowercase letters in the same column indicate significant differences at $p < 0.05$.

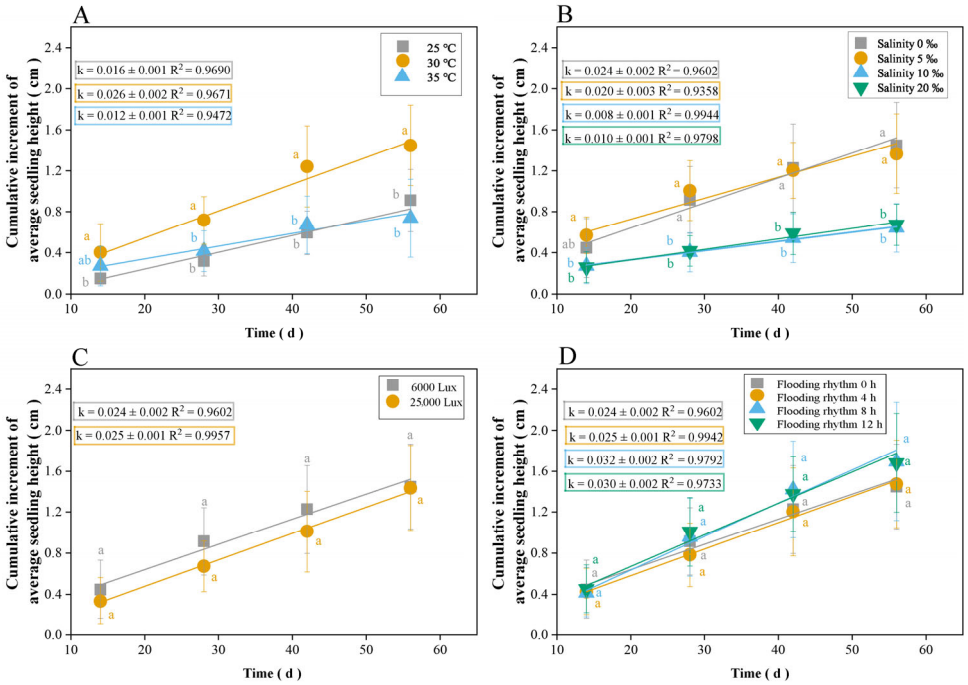


Figure 2. Cumulative mean height increment of *S. hydrophyllacea* seedlings over time: (**A**) temperature; (**B**) salinity; (**C**) light intensity; (**D**) flooding rhythm. Different lowercase letters indicate significant differences among treatments within the same period ($p < 0.05$).

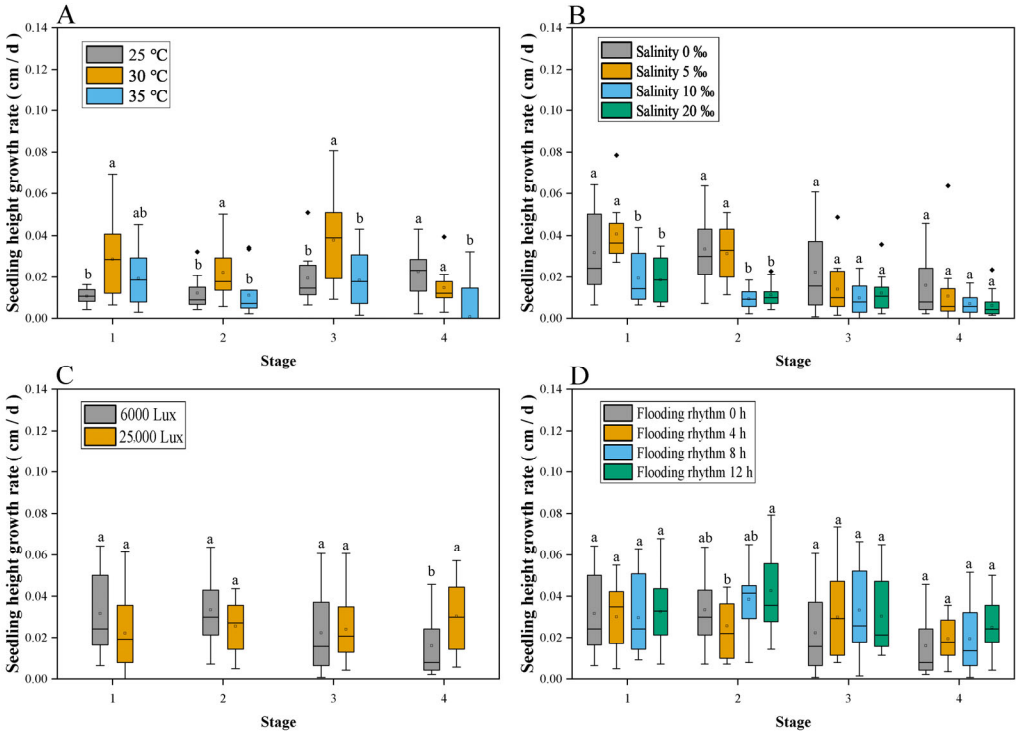


Figure 3. Height growth rates of *S. hydrophyllacea* seedlings across developmental stage: (**A**) temperature; (**B**) salinity; (**C**) light intensity; (**D**) flooding rhythm. X-axis labels (1–4) represent sequential 14-day intervals. Different lowercase letters indicate significant differences among treatments within the same period ($p < 0.05$).

3.2.2. Salinity Effects on Early Seedling Growth

Salinity significantly influenced all growth parameters except crown expansion ($p < 0.05$, $n = 15$, Table 2). Mortality peaked at 20‰ (66%), with height increment showing an inverse proportionality to salinity (Figure 2B). Growth rates in 10–20‰ treatments were significantly depressed during phases 1–2 versus controls (0–5‰, $p < 0.05$), but surviving seedlings achieved parity by phase 3 ($p > 0.05$, Figure 3B), demonstrating post-stress acclimation. Although ≤5‰ salinity yielded optimal growth, a subset (30%) of seedlings survived at 20‰ salinity, suggesting this concentration nears the species' viability threshold.

3.2.3. Light Intensity Effects on Early Seedling Growth

Crown width responded positively to high light (25,000 vs. 6000 lux, $p < 0.05$, $n = 15$), while other metrics showed no initial differences (Table 2). From phase 4 onward, 25,000 lux significantly enhanced height growth rate (Figure 3C), though cumulative height showed no significant differences across treatments (Figure 2C). This suggests that light intensity had no discernible impact on the growth of *S. hydrophyllacea* seedlings during the first three stages, but increased light intensity may promote growth in later phases.

3.2.4. Flooding Duration Effects on Early Seedling Growth

Our analysis revealed distinct flooding-duration effects on *S. hydrophyllacea* seedling morphology. As shown in Table 2 and Figure 2D, while root length and height increment remained unaffected across treatments, crown width expansion was significantly constrained (0.22 cm) under non-flooded conditions (0 h per day). The 4 h per day treatment promoted maximal leaf production (5.20 leaves), whereas height increment peaked under 8–12 h per day flooding. Notably, the 12 h per day regime induced 13.33% mortality without growth enhancement, showing 8 h per day as the optimal flooding duration for early seedling development.

3.3. Effects of Flooding Duration on One-Year-Old S. hydrophyllacea Seedlings

3.3.1. Seedling Growth and Biomass Allocation

Flooding duration induced contrasting growth responses in one-year-old *S. hydrophyllacea* seedlings. Morphological parameters (height, basal diameter, leaf number) initially increased and then decreased, peaking at 4 h of flooding, while significant suppression occurred at 12 h (Table 3). Conversely, biomass components exhibited an inverse pattern: root, stem, and leaf dry weights were at a minimum at 4 h and peaked at 12 h, with stem biomass showing particularly marked accumulation ($p < 0.05$, $n = 15$, Table 3). The root-to-shoot ratio initially decreased and then rose with prolonged flooding, showing a reduction at 4 h and a significant difference between the 0 h and 4 h treatments (Figure 4A). These findings indicate that short-term flooding (4 h) promotes morphological growth, whereas extended flooding (12 h) enhances biomass accumulation.

Table 3. Effects of flooding rhythms on growth and biomass allocation in *S. hydrophyllacea*.

Flooding Rhythm	Growth Amount			Dry Biomass			
	Seedling Height Increment (cm)	Basal Diameter Increment (mm)	Increment in Leaf Number	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Total Dry Weight (g)
0 h	11.18 ± 3.13 a	2.49 ± 0.61 ab	5.86 ± 3.29 ab	1.04 ± 0.70 a	0.53 ± 0.48 b	0.60 ± 0.23 a	2.18 ± 1.29 ab
4 h	11.80 ± 2.46 a	2.55 ± 0.62 a	7.80 ± 3.70 a	0.35 ± 0.12 a	0.40 ± 0.12 b	0.68 ± 0.05 a	1.45 ± 0.26 b
8 h	10.22 ± 2.36 a	2.70 ± 0.64 a	6.06 ± 4.43 ab	0.96 ± 0.53 a	0.83 ± 0.31 b	0.81 ± 0.34 a	2.61 ± 1.14 ab
12 h	7.56 ± 2.28 b	2.05 ± 0.73 b	4.93 ± 3.75 b	1.25 ± 0.59 a	1.03 ± 0.18 a	0.78 ± 0.28 a	3.07 ± 1.04 a

Note: Values are mean ± SD ($n = 15$). Different lowercase letters in the same column indicate significant differences at $p < 0.05$.

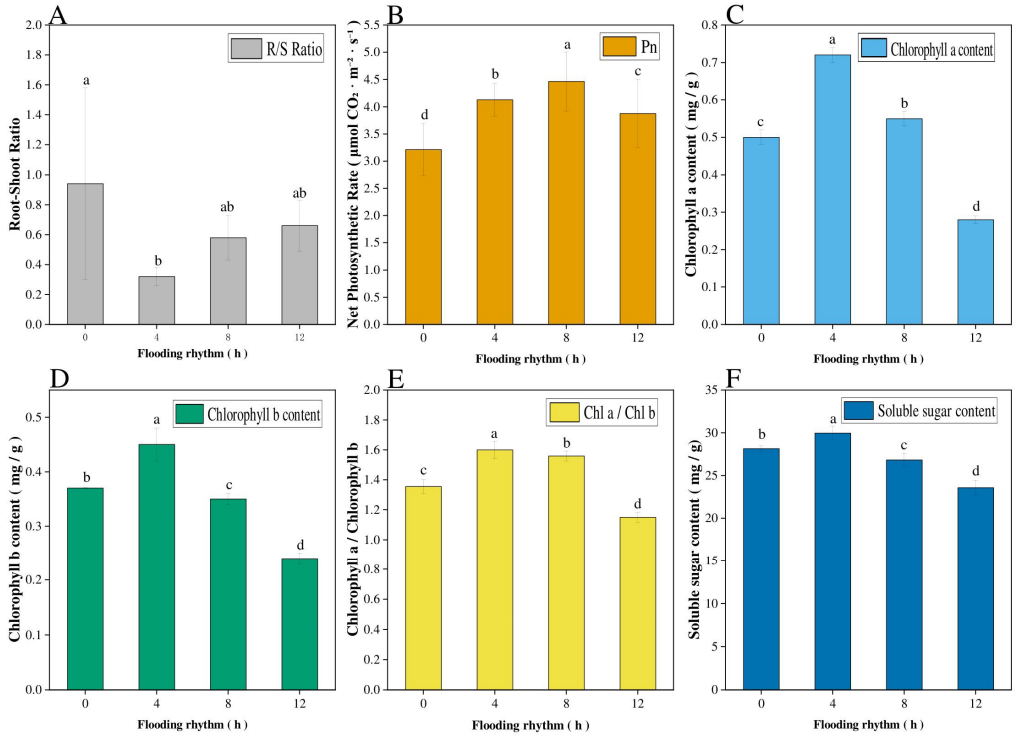


Figure 4. Effects of flooding rhythms on root–shoot ratio and physiological performance of *S. hydrophyllacea* seedling: (**A**) root–shoot ratio; (**B**) net photosynthetic rate; (**C**) chlorophyll a content; (**D**) Chlorophyll b content; (**E**) Chlorophyll a/b; (**F**) soluble sugar content. Different lowercase letters indicate significant differences at $p < 0.05$.

3.3.2. Photosynthetic Characteristics

The net photosynthetic rate (Pn) of *S. hydrophyllacea* seedlings followed a unimodal trend under increasing flooding durations, peaking at 8 h (Figure 4B), with statistically significant differences across treatments. Thus, 8 h of flooding optimally enhanced Pn, indicating that moderate flooding improves photosynthetic efficiency by optimizing light energy utilization.

3.3.3. Physiological Responses

Chlorophyll and soluble sugar content in *S. hydrophyllacea* seedlings initially increased and then decreased with prolonged flooding, peaking at 4 h but declining sharply at 12 h (Figure 4C–F). This suggests that extended flooding (12 h) may deplete soluble sugar reserves, triggering alternative stress-response metabolic pathways, while concurrently damaging photosynthetic structures.

4. Discussion

4.1. Environmental Controls on S. hydrophyllacea Seed Germination

Seed germination is a critical determinant in the conservation and restoration of the endangered mangrove species *S. hydrophyllacea*. Salinity significantly inhibited germination, likely by disrupting endogenous hormone balance, altering membrane permeability, and impairing water uptake [18]. Under optimal conditions (0‰ salinity), seeds achieved peak germination rates (41%), with both germination percentage and vigor index declining sharply as salinity increased. Conversely, the mean germination time and lag period rose markedly with higher salinity (Table 1). This aligns with observations in other mangroves (e.g., *Heritiera fomes* Banks, *Xylocarpus mekongensis* (Lam.) M.Roem., *Xylocarpus granatum* J. Koenig), which exhibit maximal germination under low or no salinity (<5‰) [19]. However, certain species (e.g., *A. marina*, 100% germination at 25‰; *Aegiceras corniculatum* (L.) Blanco, 100% radicle emergence across 0–35‰) [20] demonstrate exceptional salinity tolerance, highlighting interspecific adaptability.

Germination was most efficient at 30–35 °C, with a mean germination time decreasing significantly at elevated temperatures (Table 1). Light played a pivotal role: full-light conditions strongly promoted germination, whereas complete darkness suppressed it entirely. Notably, germination rates in growth chambers (12,000 lux; 1.3%) were significantly lower than in greenhouses (25,000 lux; 41%) (Table 1), implicating light intensity as a key regulator. Notably, when seeds of *S. hydrophyllacea* were exposed to full-light conditions in artificial incubators, their germination rate increased by 17% compared to the temperature-treated control group (mean germination rate), accompanied by enhanced germination synchrony (Table 1, Figure 1A,B). These findings underscore the combined influence of temperature, light intensity, and photoperiod on germination. Similar patterns have been reported in other species. For instance, cold-stratified *Tsuga canadensis* (L.) Carrière seeds exhibited enhanced germination at 27 °C under long photoperiods (16 h of light and 8 h of dark) [21], while dormant *Chenopodium botrys* L. seeds required elevated temperatures (25–35 °C) and extended light exposure to break dormancy [22]. Alternating temperature and light regimes (including variations in intensity and photoperiod) also overcome dormancy in highly dormant seeds like *Brassica napus* L. [23].

S. hydrophyllacea seeds exhibit a prolonged germination lag time (no germination within 30 days), indicating that viable seeds fail to germinate under favorable environmental conditions. These observations suggest that *S. hydrophyllacea* seeds exhibit dormancy. Mangrove plants are typically viviparous and thus produce non-dormant seeds. However, physical or physiological dormancy has been documented in certain mangrove species. Seeds of *Talipariti tiliaceum* (L.) Fryxell [24] and *Dendrolobium umbellatum* (L.) Benth. [25]

exhibit physical dormancy, where impermeable seed coats act as the primary barrier to germination. *Sesuvium portulacastrum* (L.) L. seeds possess fully developed embryos but require after-ripening or incubation under fluctuating temperatures to germinate [26], implying physiological dormancy. Similarly, physiological dormancy has also been documented in *Lumnitzera racemosa* Willd. and *Scaevola taccada* (Gaertn.) Roxb. [27]. Interestingly, dormancy traits may vary geographically. For example, untreated *Heritiera fomes* seeds from Sri Lanka showed complete germination failure, while excised embryos showed 67% germination; water absorption tests confirmed the absence of physical dormancy, indicating physiological dormancy in these seeds [27]. Whereas Chinese populations germinated readily (>90% within 1–2 months) [28]. Our findings demonstrate that *S. hydrophyllacea* seeds exhibit dormancy characteristics, but further studies are needed to clarify the type of dormancy in *S. hydrophyllacea*.

4.2. Stress Effects on S. hydrophyllacea Seedling Growth Performance

Environmental factors differentially regulate the growth of *S. hydrophyllacea* seedlings. Thermal adaptation studies identified 30 °C as the optimal temperature for leaf growth, consistent with observations in *Rhizophora stylosa* Griff. [29]. Salinity stress significantly inhibited the growth of *S. hydrophyllacea* seedlings, with progressive reductions in height increment, leaf number, and root length as salinity increased. Elevated salinity generally increases mortality rates in mangrove seedlings [30]. However, co-occurring mangroves like *Bruguiera sexangula* (Lour.) Poir. and *C. tagal* maintain 70%–80% survival at 30‰ salinity [31,32] and *B. gymnorrhiza* thrives at 10‰ [33]. *L. racemosa.* shows optimal growth at 15–25‰ salinity, with survival rates declining markedly above 35‰ [34]. *Excoecaria agallocha* L. seedlings thrive at 0–5‰ salinity, while mature trees tolerate up to 15‰ [35]. In contrast, *S. hydrophyllacea* seedlings exhibited mortality at >5‰, reaching 66% at 20‰ (Table 2). This underscores their lower saline adaptability compared to sympatric species, confirming salinity as a critical recruitment bottleneck [8].

Furthermore, the salt stress response in *S. hydrophyllacea* seedlings exhibited distinct developmental phases. Height growth rates differed significantly across salinity treatments during the first month but converged by the second month (Figure 3B), suggesting progressive enhancement of salt tolerance during ontogeny. Pranchai (2025) demonstrated that artificial macro-pores mimicking crab burrows can significantly improve survival rates of *Bruguiera cylindrica* (L.). Blumeseedlings by enhancing soil aeration, water infiltration, and salt leaching [36]. This approach may provide a viable strategy for facilitating early establishment and population restoration of *S. hydrophyllacea* seedlings in high-salinity habitats.

Under waterlogging stress, plants exhibit varying degrees of morphological modifications depending on their species-specific tolerance. Generally, flood-intolerant species show limited morphological changes, whereas flood-tolerant species develop adaptive morphological modifications [37]. As inhabitants of the intertidal zone, mangrove plants benefit from moderate waterlogging, whereas prolonged submergence retards their growth [38]. Biomass allocation serves as a key indicator of environmental adaptation, clearly reflecting the resource partitioning strategies of seedlings under different waterlogging regimes. Juvenile seedlings (1–2 months post-germination) showed increased height and crown expansion with longer waterlogging duration. Maximum growth occurred at 12 h per day treatment. However, this group showed a mortality rate of 13.33%, while the 8 h per day treatment maintained comparable growth without any mortality, indicating 8 h per day as the optimal duration for juvenile seedlings. In contrast, one-year-old seedlings exhibited rapid height and basal diameter increases under short-term (4 h per day) waterlogging, indicative of an escape strategy mediated by ethylene-induced elongation [39]. Concurrently, the 4 h treatment showed peak chlorophyll a/b and soluble sugar contents, suggesting

enhanced photosynthetic capacity and sugar metabolism to support rapid growth under short-term stress. This response aligns with the carbon allocation priority hypothesis, where plants preferentially allocate photosynthates to growth-related organs under mild stress rather than long-term storage [40].

Seedlings subjected to intermediate waterlogging (8 h) exhibited distinct physiological characteristics. Although the photosynthetic rate peaked, the chlorophyll content and soluble sugars had already begun to decline, suggesting a shift from growth to stress resistance [41]. The elevated photosynthetic rate may represent a compensatory mechanism under sustained stress, enhancing light-use efficiency to offset energy losses, consistent with the photosynthetic compensation hypothesis [42]. Prolonged waterlogging (12 h per day) elicited tolerance traits—maximized biomass but suppressed metabolism (e.g., minimal chlorophyll/sugars)—consistent with resource reallocation to structural reinforcement under chronic hypoxia [43–45].

Therefore, the optimal daily waterlogging duration for one-year-old seedlings was determined to be 4–8 h per day. The optimal waterlogging duration for *S. hydrophyllacea* was significantly shorter than that of typical low-intertidal species. For instance, the optimal waterlogging durations were 8–12 h per day for *A. marina* [46], 8–12 h per day for *Aegiceras Gaertn.* [47], and up to 12 h per day for *B. gymnorrhiza* [48]. This difference likely reflects *S. hydrophyllacea*'s predominant distribution in mid–high intertidal zones.

5. Conclusions

This study demonstrates that the reproductive success of the endangered mangrove *S. hydrophyllacea* is critically constrained by interacting environmental stressors. (1) Germination and early growth: 30–35 °C is the optimal germination temperature, but seedling mortality reached 73.3% at 35 °C, highlighting vulnerability to heat extremes. Both light intensity and photoperiod positively regulate germination, with optimal seed germination occurring under full-light conditions. Salinity is the primary limiting factor. Germination thrives in low-salinity conditions (<5‰), whereas $\geq$ 20‰ causes 66% seedling mortality, severely restricting recruitment. (2) Waterlogging adaptations: Short-term flooding (4–8 h per day) enhances growth (height, diameter, leaf number) and photosynthesis (peak net rate at 8 h). Prolonged flooding (12 h per day) triggers stress responses: biomass shifts to roots (highest root–shoot ratio), while chlorophyll and sugars decline, indicating photostructural damage and metabolic suppression. (3) Conservation implications: Climate change-driven sea-level rise and temperature extremes may exacerbate habitat salinization and thermal stress, further threatening natural regeneration of *S. hydrophyllacea*. We propose urgent interventions (artificial propagation and screening for stress-resistant genotypes) and long-term monitoring to assess the adaptive capacity of this species under shifting climate regimes.

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