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Optimisation of seed germination and seedling cultivation conditions for *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* in a plant factory

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Abstract: *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* are key mangrove species, but their populations have declined recently due to human activities. To promote their restoration, this study optimised seed germination and seedling cultivation using the plant factory method. The parameters, such as illumination, salinity, temperature and nutrient conditions, were examined. Our results showed that suitable illumination, salinity and temperature promoted seed germination of both species. Nutrient addition promoted the germination of *B. gymnorrhiza* but had little effect on *A. ilicifolius*. Both species of seedlings grew best in short illumination duration and moderate illumination intensity. Although both species can tolerate high salinity, low salinity (0–10‰ for *B. gymnorrhiza* and 0–5‰ for *A. ilicifolius*) promoted seedlings' growth. High temperature (28–32°C) accelerated the growth of both species of seedlings. Nutrient addition enhanced the growth of both species' seedlings, especially the addition of $\text{Ca}^{2+}/\text{Mg}^{2+}$ and trace elements strongly promoted the growth of *B. gymnorrhiza* seedlings. We obtained optimal conditions for seed germination and seedling growth of both species in the plant factory, demonstrating that environmental control significantly enhanced their germination and growth rates. Our findings provide valuable insights into the efficiency of mangrove restoration and the sustainable development of mangrove ecosystems.

Keywords: illumination; mangrove species; nutrient; restoration; salinity, temperature

Mangroves are unique wetland ecosystems found in tropical and subtropical coastal areas, playing a crucial role in protecting coastlines and maintaining biodiversity (Kathiresan 2021). However, many mangrove habitats have been lost recently due to human activities and natural losses (Xu et al. 2024). To support the restoration of mangroves, the efficient cultivation of mangrove seedlings is essential.

A plant factory is an advanced agricultural system characterised by high automation, precise environmental control, and efficient space utilisation, regulating illumination, temperature, humidity, nutrients,

and CO_2 concentration to optimise plant growth (Benke, Tomkins 2017). Currently, plant factories are widely used for cultivating vegetables, flowers and other herbaceous plants. For example, the growth of vegetables (chicory, green mizuna, radish and alfalfa) and flowers (French marigold and celosia) was promoted in a plant factory (Orlando et al. 2022). However, few studies have focused on seed germination and seedling cultivation of woody plants.

Bruguiera gymnorrhiza is a viviparous mangrove while *Acanthus ilicifolius* is nonviviparous (Liu et al. 2025). Currently, seed germination and seedling

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cultivation of mangrove plants mainly rely on outdoor nurseries, which are subject to uncontrollable environmental factors such as illumination, temperature, soil types and salinity (Khan et al. 2024). Therefore, this study aims to identify the optimal illumination, salinity, temperature and nutrition conditions for seed germination and seedling cultivation of both species in plant factory systems.

MATERIAL AND METHODS

Plant materials and a plant factory culture device. *B. gymnorrhiza* and *A. ilicifolius* seeds were collected from Qinzhou, Guangxi Province, China. The schematic diagram and photograph of the plant factory culture device are shown in Figure S1 in electronic supplementary material (ESM). The size of the device (two layers) is 2 m in length, 1.2 m in width and 2 m in height. The light source was a top-mounted LED module (Sanan M-Series, China) with a red/blue/green light ratio of 8 : 3 : 1. An air conditioner was used to control room temperature. The culture substrate for *B. gymnorrhiza* consisted of a 1 : 1 mixture of sea mud and sand, while *A. ilicifolius* was a sand substrate.

Experiment settings of illumination duration, illumination intensity, salinity and temperature. For the seed experiment, illumination durations for both species were set to 0, 6, 12 and 18 h/day. For the seedling experiment, seedlings of similar shoot heights and leaves were selected for both species, and illumination durations were set to 8, 12, 16 and 20 h/day. Illumination intensities for both species (seed and seedling experiments) were set at 50, 100, 200 and 400 $\mu\text{mol}/\text{m}^2/\text{s}$.

The commercial sea salt (Qingdao Sea Salt Aquarium Technology Co., Ltd., China) was used as a source of salinity. Salinities for *B. gymnorrhiza* were set to 0, 10, 15 and 25‰, while *A. ilicifolius* were set to 0, 5, 10, 15 and 25‰. For both species, the culture substrate for the salinity experiment was sand. Temperatures for both species were set to 20, 24, 28 and 32 °C.

Experiment settings of nutrient conditions. The Stanley compound fertiliser (Stanley Fertilizer Co., Ltd., China; 15% N, 15% P_2O_5 and 15% K_2O) was used for *B. gymnorrhiza*, while Yuanlv organic fertiliser (Yuanlv Agricultural Technology Co., Ltd., China; 9.91% N, 2.36% P_2O_5 , 2.50% K_2O and organic matter $\geq 52\%$) was used for *A. ilicifolius*. For the seed experi-

ment, Stanley was added to *B. gymnorrhiza* at concentrations of 0, 0.03, 0.06, 0.12, 0.24, and 0.48 g/kg substrate, and Yuanlv was added to *A. ilicifolius* at concentrations of 0, 0.675, 1.35, 2.70, 5.39, 10.77, 21.54, and 32.31 g/kg substrate. For the seedling experiment, Stanley was added to *B. gymnorrhiza* at 0, 0.27, 0.53, 1.07 and 1.60 g/kg substrate for every 20 days, and Yuanlv was added to *A. ilicifolius* at 0, 2.70, 5.39, 10.77 and 21.54 g/kg substrate for every 45 days.

$\text{Ca}^{2+}/\text{Mg}^{2+}$ and trace elements were added at 0 \times , 0.5 \times , 1 \times , 2 \times and 3 \times for every 20 days (*B. gymnorrhiza*) and 45 days (*A. ilicifolius*).

The formulation of $\text{Ca}^{2+}/\text{Mg}^{2+}$ (1 \times) and trace elements (1 \times) followed the modified Hoagland nutrient solution formula. The formulations of $\text{Ca}^{2+}/\text{Mg}^{2+}$ and trace elements (0 \times , 0.5 \times , 1 \times , 2 \times and 3 \times) were shown in Table S1 in ESM.

Sample collection and growth indicator measurement. Each experimental group had three replicates. Each replicate contained 7–8 seeds (5 seeds for the temperature experiment) or 3–6 seedlings of *B. gymnorrhiza*, and 12–18 seeds or 6–8 seedlings of *A. ilicifolius*. After 90–120 days of cultivation, seedlings were harvested to measure growth indicators and chlorophyll content (95% ethanol extraction method) (Ferreira et al. 2021).

The apparent growth indicators were germination rate (number of germinated seeds/total seeds), shoot height increment, leaf length increment (longitudinal length of the largest leaf), leaf width increment (transverse length of the largest leaf) and leaf number increment.

Statistical analysis. The significance tests and one-way ANOVA were performed using SPSS software version 27. When significant differences were found ($P < 0.05$), multiple comparisons were conducted using the Duncan method. Data were presented as the mean \pm standard error, with different letters indicating significant differences ($P < 0.05$).

RESULTS

Germination of *B. gymnorrhiza* and *A. ilicifolius* under different illumination durations, illumination intensities, salinities and temperatures. The germination rate and speed of *B. gymnorrhiza* were the highest under illumination durations of 18 h/day, with a germination rate of 100% on day 50. Meanwhile, the germination rate and speed of *A. ilicifolius* were the highest under illumination dura-

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tions of 6 h/day, with a germination rate of 93.75% on day 22 (Figures 1A and 1B).

The germination rate and speed of *B. gymnorrhiza* were the highest under illumination intensity of 400 $\mu\text{mol}/\text{m}^2/\text{s}$, with a germination rate of 95.83% on day 59. Meanwhile, the germination rate and speed of *A. ilicifolius* were the highest under illumination intensity of 100 $\mu\text{mol}/\text{m}^2/\text{s}$, with a germination rate of 91.67% on day 29 (Figures 1C and 1D).

The germination rate and speed of *B. gymnorrhiza* were the highest under 10‰ salinity, with a germination rate of 100% on day 29. Meanwhile, the germination rate and speed of *A. ilicifolius* were the highest under 5‰ salinity, with a germination rate of 100% on day 21 (Figures 1E and 1F).

The germination rate and speed of *B. gymnorrhiza* were the highest under 28 °C, with a germination rate of 100% on day 57. Meanwhile, the germination rate and speed of *A. ilicifolius* were the highest under 32 °C, with a germination rate of 100% on day 17 (Figures 1G and 1H).

Germination of *B. gymnorrhiza* and *A. ilicifolius* under different nutrient conditions. The germination rate and speed of *B. gymnorrhiza* were the highest at a substrate concentration of 0.03 g/kg with Stanley commercial fertiliser, with a germination rate of 95.83% on day 18. Meanwhile, the germination rate and speed of *A. ilicifolius* were the highest under a substrate of 5.39 g/kg Yuanlv commercial fertiliser, with a germination rate of 100% on day 17 (Figures 2A and 2B).

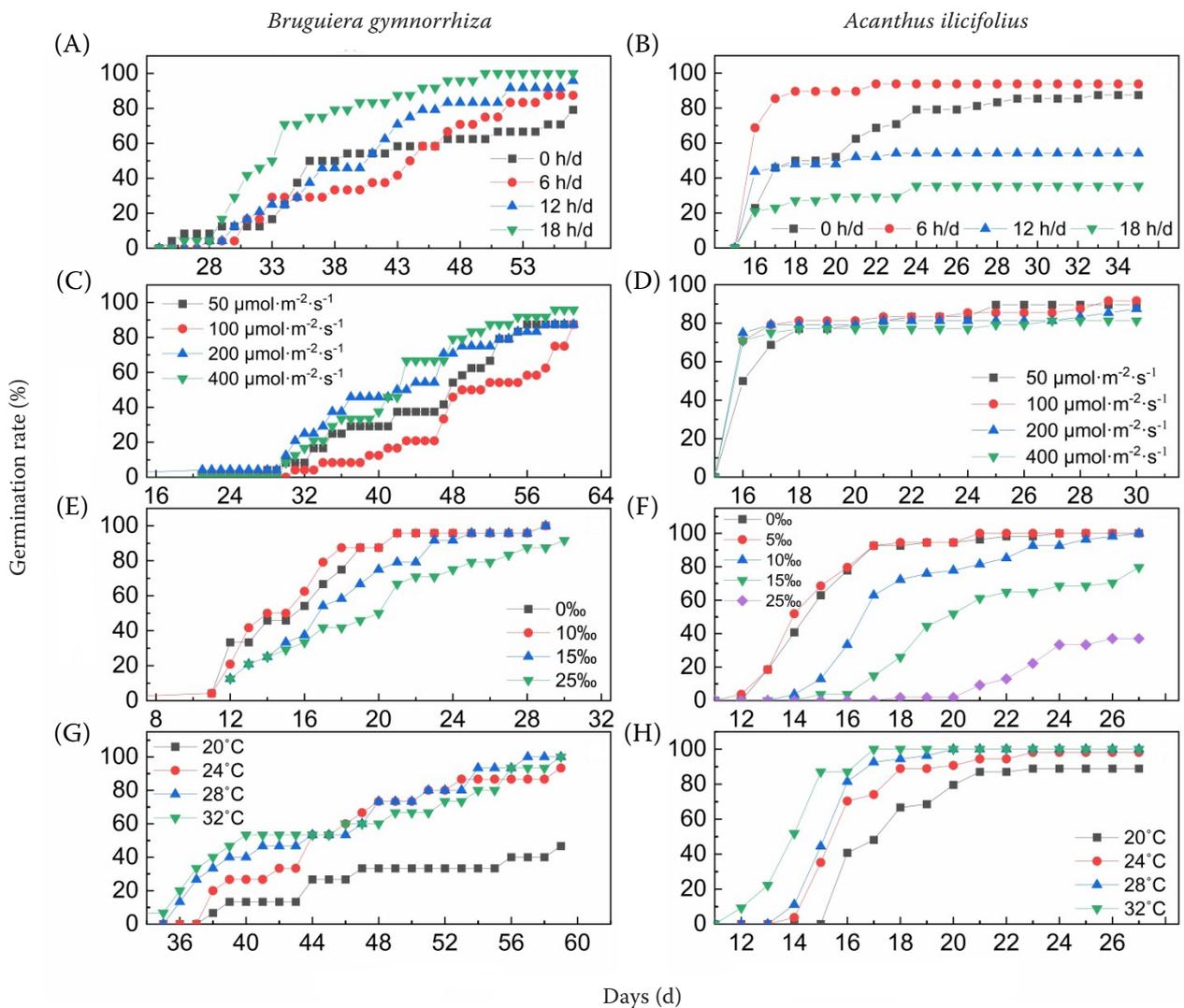


Figure 1. Germination rates of *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* seeds under different (A, B) illumination durations, (C, D) illumination intensities, (E, F) salinities and (G, H) temperatures

The germination rate and speed of *B. gymnorrhiza* were the highest under $2\times \text{Ca}^{2+}/\text{Mg}^{2+}$, with a germination rate of 100% on day 57. Meanwhile, the germination rate and speed of *A. ilicifolius* were the highest under $0.5\times \text{Ca}^{2+}/\text{Mg}^{2+}$, with a germination rate of 100% on day 21 (Figures 2C and 2D).

The germination rate and speed of *B. gymnorrhiza* were the highest under $0.5\times$ trace elements, with a germination rate of 100% on day 57. Meanwhile, the germination rate and speed of *A. ilicifolius* were similar at different additions of trace elements, with a germination rate of 100% on day 22 to 23 (Figures 2E and 2F).

Growth indicators and chlorophyll content of *B. gymnorrhiza* and *A. ilicifolius* under different illumination durations, illumination intensities, salinities and temperatures. For *B. gymnorrhiza*, the most significant increments in shoot height (5.13 ± 0.35 cm/plant), leaf length (7.69 ± 0.55 cm/leaf), leaf width (3.57 ± 0.18 cm/leaf) and leaf number (4.13 ± 1.00 leaves/plant) occurred at an illumination duration of 8 h/day. For *A. ilicifolius*, the most significant increments in shoot height (1.45 ± 0.08 cm/plant) and leaf

length (5.07 ± 0.52 cm/leaf) occurred at an illumination duration of 8 h/day, while the most significant increments in leaf width (2.21 ± 0.07 cm/leaf) and leaf number (5.33 ± 0.61 leaves/plant) occurred at an illumination duration of 12 h/day (Figures 3A–3D). Moreover, the highest contents of chlorophyll *a* (1.40 ± 0.12 mg/g FW), chlorophyll *b* (0.60 ± 0.08 mg/g FW) and total chlorophyll (2.00 ± 0.20 mg/g FW) of *B. gymnorrhiza* occurred at an illumination duration of 20 h/day. The highest contents of chlorophyll *a* (0.52 ± 0.05 mg/g FW), chlorophyll *b* (0.22 ± 0.02 mg/g FW) and total chlorophyll (0.74 ± 0.07 mg/g FW) of *A. ilicifolius* occurred at an illumination duration of 8 h/day (Figure S2 in ESM).

For *B. gymnorrhiza*, the most significant increments in shoot height (9.91 ± 1.09 cm/plant), leaf length (11.34 ± 0.09 cm/leaf), leaf width (4.61 ± 0.14 cm/leaf), and leaf number (6.00 ± 0.00 leaves/plant) occurred at an illumination intensity of $100 \mu\text{mol}/\text{m}^2/\text{s}$. For *A. ilicifolius*, the most significant increments in shoot height (1.72 ± 0.07 cm/plant), leaf length (5.70 ± 0.72 cm/leaf), leaf width (2.47 ± 0.47 cm/leaf), and leaf number (7.07 ± 0.23 leaves/plant) occurred

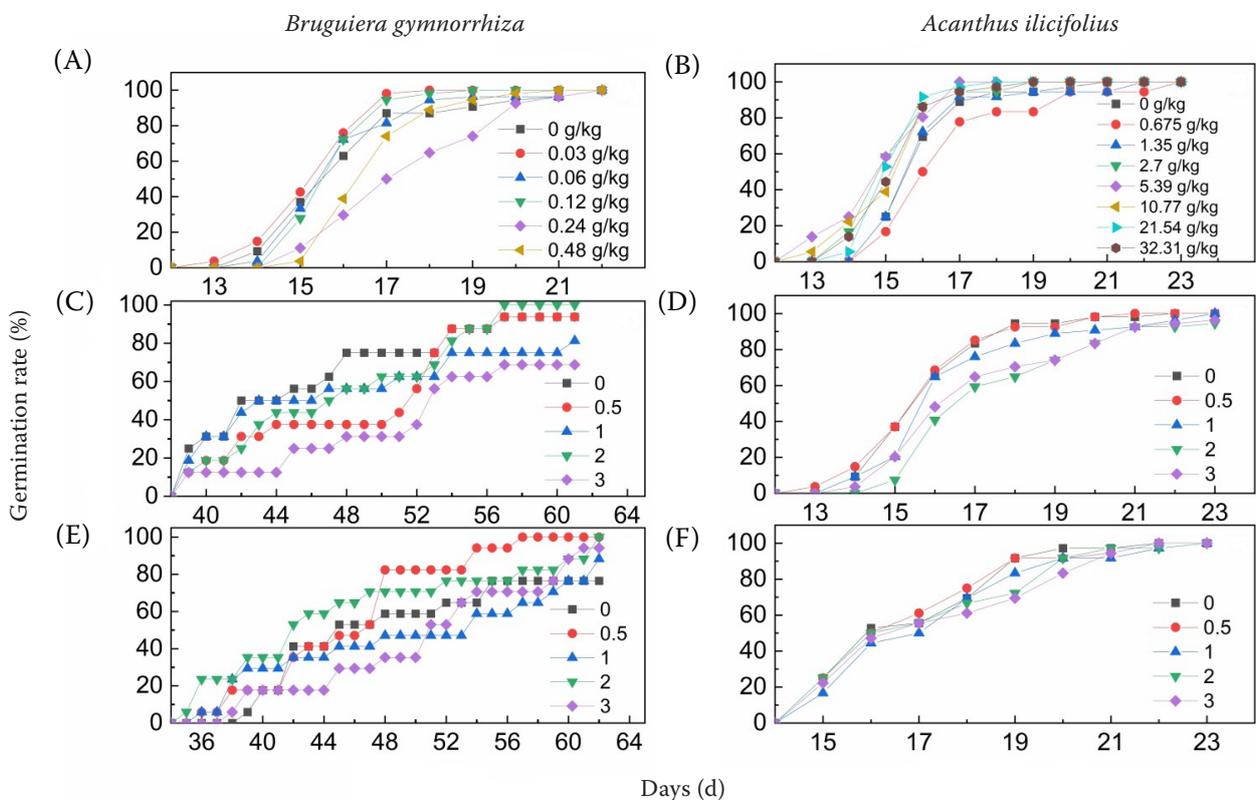


Figure 2. Germination rates of *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* seeds under different additions of (A, B) commercial fertiliser, (C, D) $\text{Ca}^{2+}/\text{Mg}^{2+}$ and (E, F) trace elements

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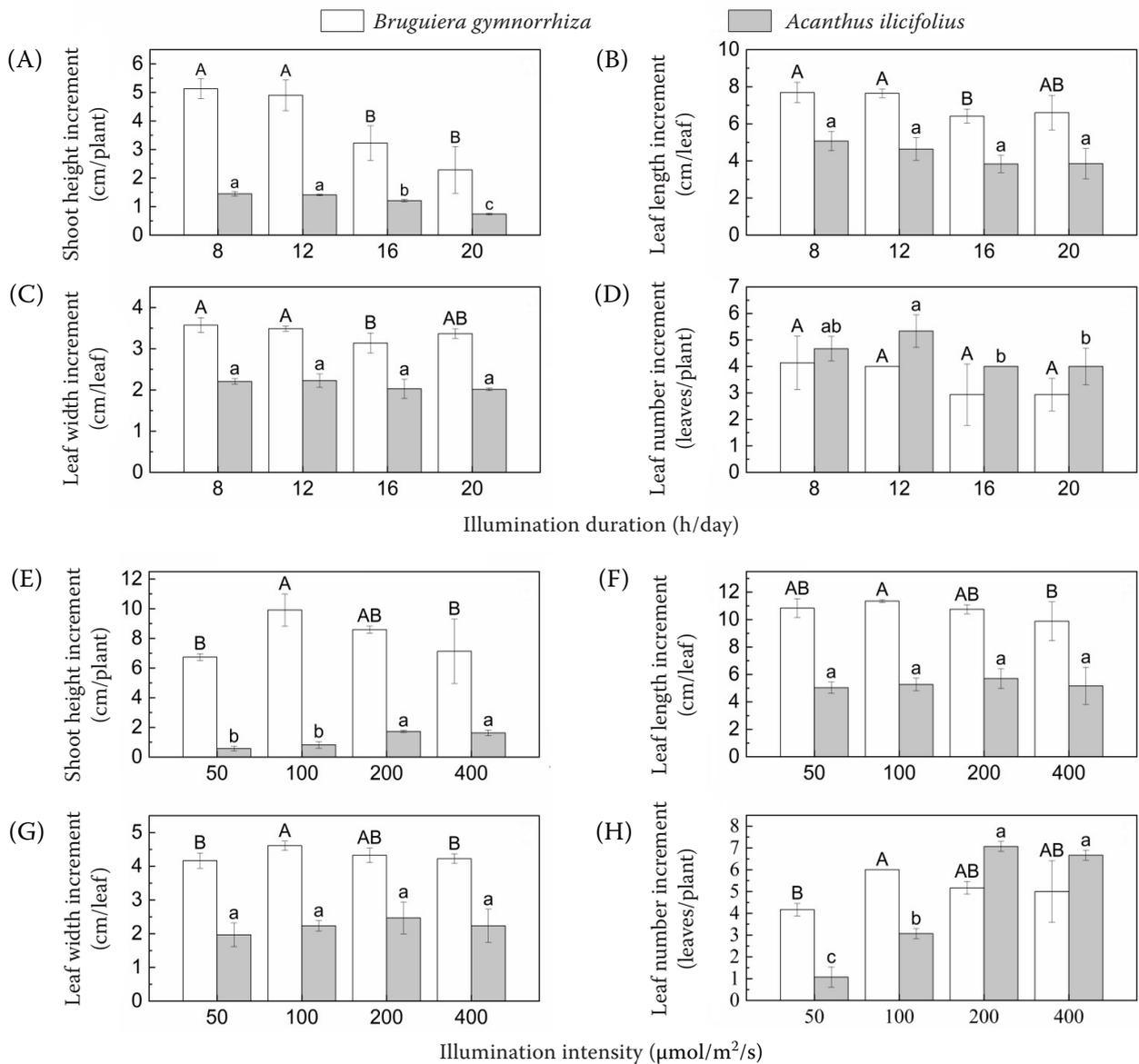


Figure 3. Apparent growth indicators of *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* seedlings under different illumination (A–D) durations and (E–H) intensities

^{a,b,c}different letters indicate significant differences ($P < 0.05$); ^{A,B}different letters indicate significant differences ($P < 0.05$)

at an illumination intensity of 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (Figures 3E–3H). Moreover, the highest contents of chlorophyll *a* (1.31 ± 0.14 mg/g FW), chlorophyll *b* (0.54 ± 0.06 mg/g FW), and total chlorophyll (1.86 ± 0.20 mg/g FW) of *B. gymnorrhiza* occurred at an illumination intensity of 200 $\mu\text{mol}/\text{m}^2/\text{s}$. Similarly, the highest contents of chlorophyll *a* (0.73 ± 0.02 mg/g FW), chlorophyll *b* (0.33 ± 0.01 mg/g FW), and total chlorophyll (1.05 ± 0.03 mg/g FW) of *A. ilicifolius* occurred at an illumination intensity of 200 $\mu\text{mol}/\text{m}^2/\text{s}$ (Figure S2 in ESM).

For *B. gymnorrhiza*, the most significant increments in shoot height (10.32 ± 0.22 cm/plant), leaf length (11.21 ± 0.54 cm/leaf), and leaf number (7.78 ± 0.56 leaves/plant) occurred at 10‰ salinity, while the most significant increment in leaf width (4.86 ± 0.08 cm/leaf) occurred at 0‰ salinity. For *A. ilicifolius*, the most significant increments in shoot height (4.20 ± 0.15 cm/plant), leaf width (2.44 ± 0.13 cm/leaf), and leaf number (6.00 ± 0.00 leaves/plant) occurred at 5‰ salinity, while the most significant increment in leaf length (6.07 ± 0.58 cm/leaf) occurred at 0‰ salin-

ity (Figures 4A–4D). Moreover, the highest contents of chlorophyll *a* (1.35 ± 0.26 mg/g FW), chlorophyll *b* (0.62 ± 0.18 mg/g FW), and total chlorophyll (1.97 ± 0.44 mg/g FW) of *B. gymnorrhiza* occurred at 10‰ salinity. The highest contents of chlorophyll *a* (2.08 ± 0.14 mg/g FW), chlorophyll *b* (0.80 ± 0.05 mg/g FW), and total chlorophyll (2.88 ± 0.19 mg/g FW) of *A. ilicifolius* occurred at 5‰ salinity (Figure S3 in ESM).

For *B. gymnorrhiza*, the most significant increments in shoot height (10.33 ± 0.83 cm/plant) and leaf number (5.60 ± 0.40 leaves/plant) oc-

curred at 32 °C, the most significant increments in leaf length (6.68 ± 0.45 cm/leaf) and leaf width (3.43 ± 0.08 cm/leaf) occurred at 24 °C. For *A. ilicifolius*, the most significant increments in shoot height (7.84 ± 0.48 cm/plant) and leaf number (5.75 ± 0.00 leaves/plant) occurred at 32 °C, the most significant increments in leaf length (6.21 ± 0.29 cm/leaf) and leaf width (2.51 ± 0.04 cm/leaf) occurred at 28 °C (Figures 4E–4H).

Moreover, the highest contents of chlorophyll *a* (1.45 ± 0.03 mg/g FW), chlorophyll *b* (0.54 ± 0.01 mg/g FW), and total chlorophyll

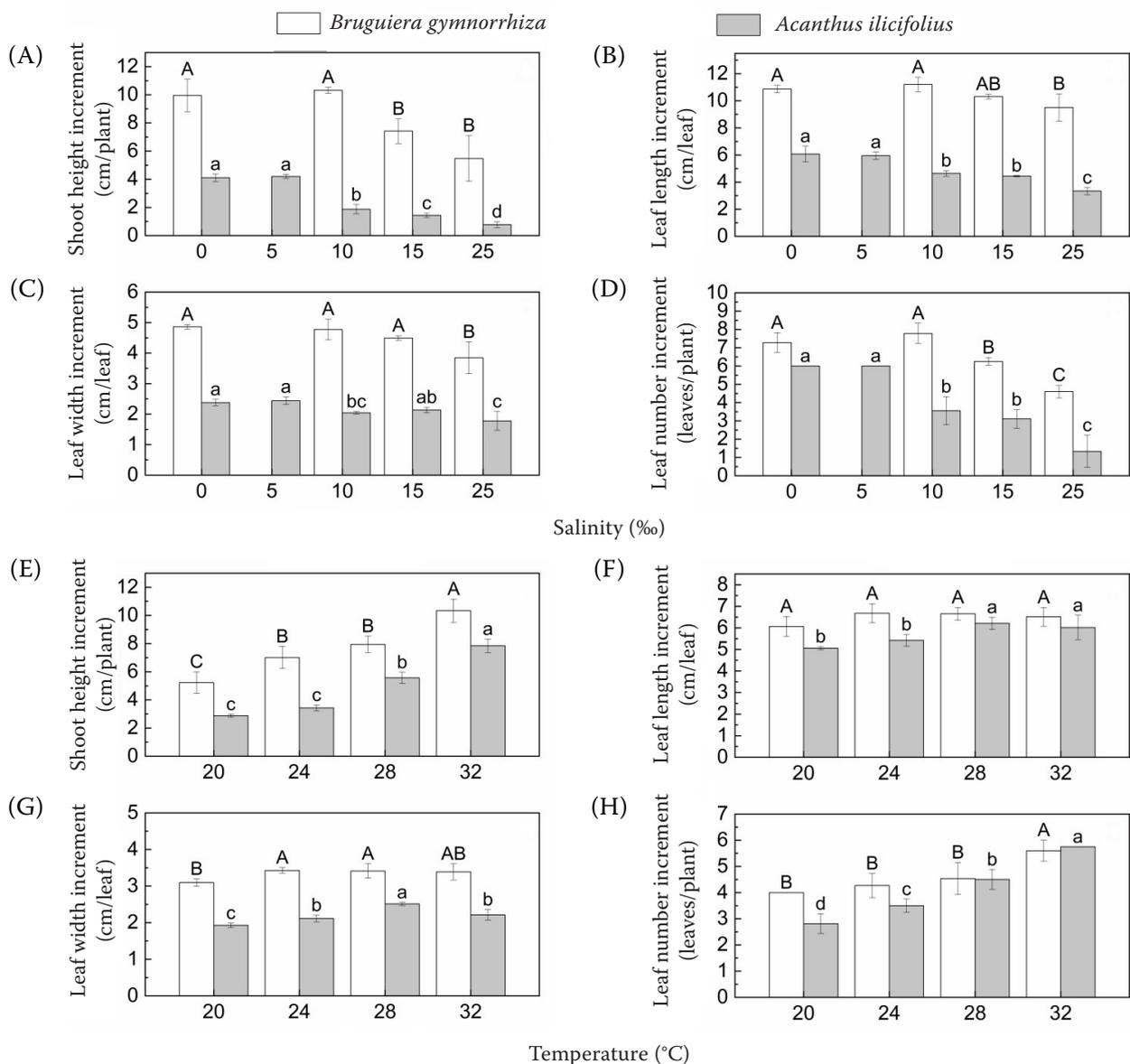


Figure 4. Apparent growth indicators of *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* seedlings under different (A–D) salinities and (E–H) temperatures

^{a–d}different letters indicate significant differences ($P < 0.05$); ^{A,B,C}different letters indicate significant differences ($P < 0.05$)

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(0.54 ± 0.01 mg/g FW) of *B. gymnorrhiza* occurred at 32 °C. Similarly, the highest contents of chlorophyll *a* (2.00 ± 0.40 mg/g FW), chlorophyll *b* (0.79 ± 0.14 mg/g FW), and total chlorophyll (2.79 ± 0.55 mg/g FW) of *A. ilicifolius* occurred at 32 °C (Figure S3 in ESM).

Growth indicators and chlorophyll content of *B. gymnorrhiza* and *A. ilicifolius* under different nutrient conditions. For *B. gymnorrhiza*, the most significant increments in shoot height (8.97 ± 0.50 cm/plant), leaf length (10.97 ± 0.63 cm/leaf), leaf width (4.41 ± 0.36 cm/leaf), and leaf number (5.72 ± 0.35 leaves/plant) occurred at 0.53 g/kg substrate of Stanley commercial fertiliser. For *A. ilicifolius*, the most significant increments in shoot height (4.78 ± 0.99 cm/plant), leaf length (5.44 ± 0.14 cm/leaf), and leaf width (2.25 ± 0.09 cm/leaf) occurred at 5.39 g/kg substrate of Yuanlv commercial fertiliser, while the most significant increment in leaf number (3.67 ± 0.38 leaves/plant) occurred at 10.77 g/kg substrate of Yuanlv commercial fertiliser (Figure 5). Moreover, for *B. gymnorrhiza*, the highest content of chlorophyll *a* (1.23 ± 0.06 mg/g FW) occurred at 1.60 g/kg substrate of Stanley com-

mercial fertiliser, while the highest contents of chlorophyll *b* (0.86 ± 0.16 mg/g FW) and total chlorophyll (2.04 ± 0.17 mg/g FW) occurred at 0.53 g/kg substrate of Stanley commercial fertiliser. For *A. ilicifolius*, the highest contents of chlorophyll *a* (0.95 ± 0.15 mg/g FW), chlorophyll *b* (0.47 ± 0.15 mg/g FW), and total chlorophyll (1.42 ± 0.20 mg/g FW) occurred at 5.39 g/kg substrate of Yuanlv commercial fertiliser (Figure S4 in ESM).

For *B. gymnorrhiza*, the most significant increments in shoot height (10.60 ± 0.90 cm/plant), leaf length (11.87 ± 0.23 cm/leaf), leaf width (5.03 ± 0.52 cm/leaf), and leaf number (8.67 ± 0.00 leaves/plant) occurred at $0.5 \times \text{Ca}^{2+}/\text{Mg}^{2+}$. For *A. ilicifolius*, the most significant increment in shoot height (3.73 ± 0.12 cm/plant), leaf length (5.52 ± 0.20 cm/leaf), and leaf number (2.75 ± 0.50 leaves/plant) occurred at $3 \times \text{Ca}^{2+}/\text{Mg}^{2+}$, while the most significant increments in leaf width (2.39 ± 0.50 cm/leaf) occurred at $0.5 \times \text{Ca}^{2+}/\text{Mg}^{2+}$ (Figures 6A–6D). Moreover, the highest contents of chlorophyll *a* (1.58 ± 0.22 mg/g FW), chlorophyll *b* (0.96 ± 0.27 mg/g FW), and total chlorophyll (2.54 ± 0.48 mg/g FW) of *B. gymnorrhiza* occurred at $2 \times \text{Ca}^{2+}/\text{Mg}^{2+}$. Similarly, the highest contents of chlorophyll *a* (0.77 ± 0.01 mg/g FW), chloro-

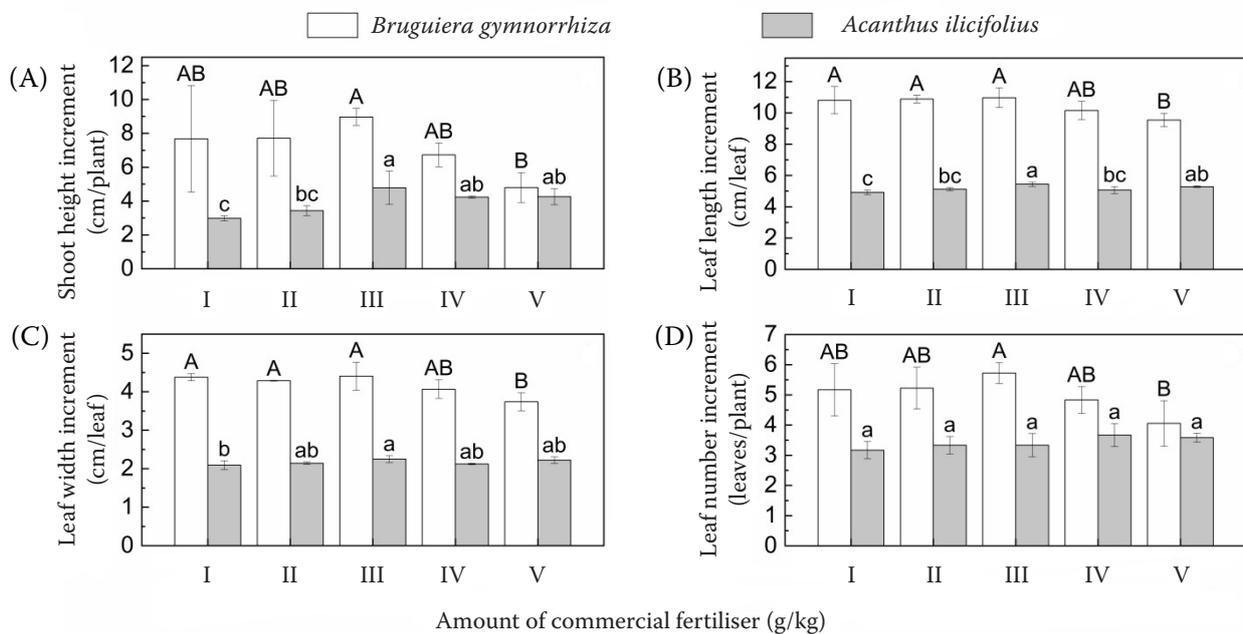


Figure 5. Apparent growth indicators of *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* seedlings under different additions of commercial fertiliser

I–V – different additive amounts of fertiliser for *B. gymnorrhiza* (0, 0.27, 0.53, 1.07 and 1.60 g/kg substrate of Stanley commercial fertiliser, respectively), and for *A. ilicifolius* (0, 2.70, 5.39, 10.77 and 21.54 g/kg substrate of Yuanlv commercial fertiliser, respectively)

^{a,b,c}different letters indicate significant differences ($P < 0.05$); ^{A,B}different letters indicate significant differences ($P < 0.05$)

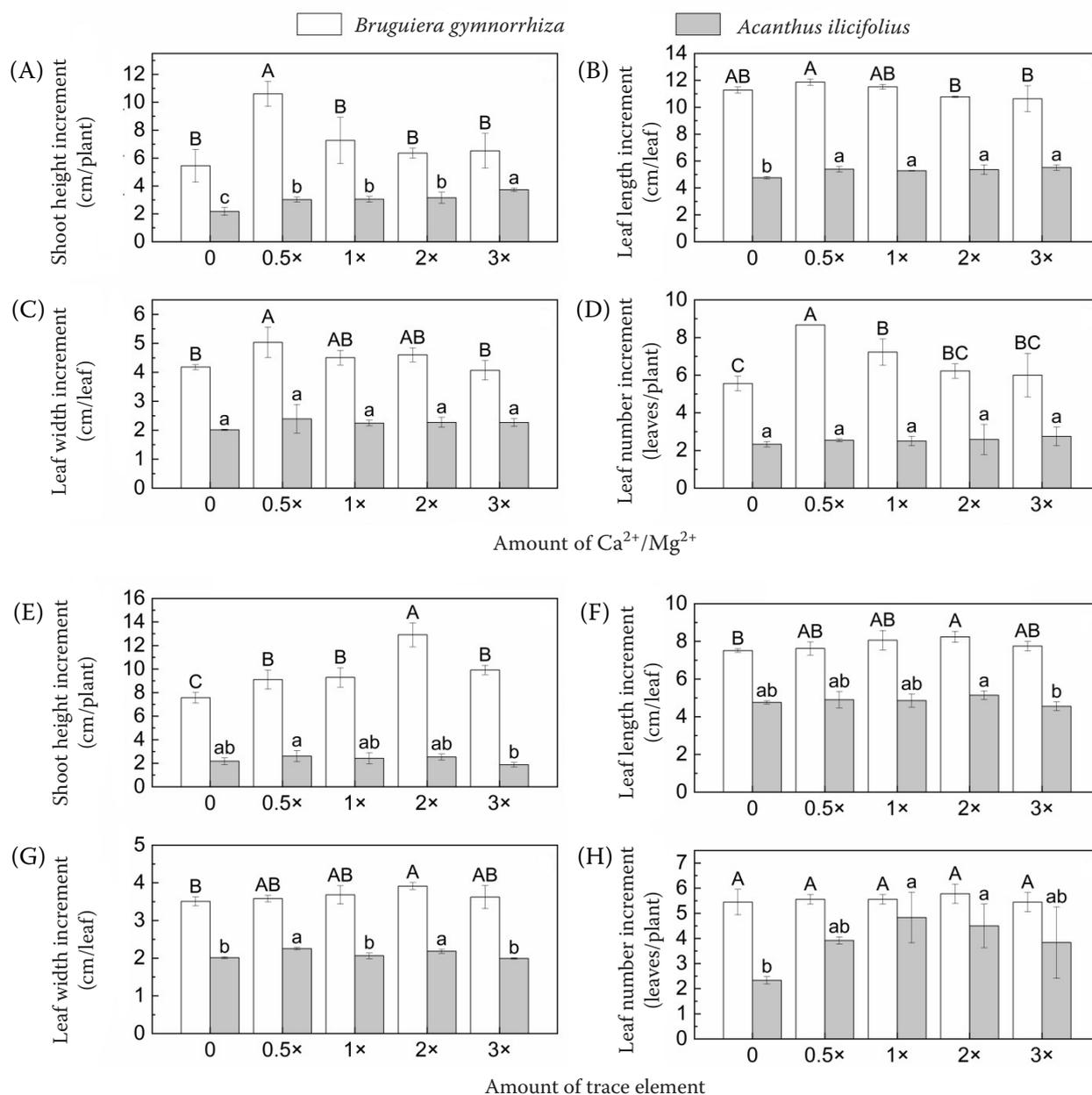


Figure 6. Apparent growth indicators of *Bruguiera gymnorrhiza* and *Acanthus ilicifolius* seedlings under different additions of (A–D) $\text{Ca}^{2+}/\text{Mg}^{2+}$ and (E–H) trace elements a, b, c different letters indicate significant differences ($P < 0.05$); A, B, C different letters indicate significant differences ($P < 0.05$)

phyll *b* (0.35 ± 0.01 mg/g FW), and total chlorophyll (1.12 ± 0.01 mg/g FW) of *A. ilicifolius* occurred at $2\times$ $\text{Ca}^{2+}/\text{Mg}^{2+}$ (Figure S5 in ESM).

For *B. gymnorrhiza*, the most significant increments in shoot height (12.91 ± 1.01 cm/plant), leaf length (8.24 ± 0.29 cm/leaf), leaf width (3.91 ± 0.09 cm/leaf), and leaf number (5.78 ± 0.38 leaves/plant) occurred at $2\times$ trace elements. For *A. ilicifolius*, the most significant increments in shoot height (2.61 ± 0.47 cm/plant) and leaf

width (2.25 ± 0.03 cm/leaf) occurred at $0.5\times$ trace elements, while the most significant increment in leaf length (5.14 ± 0.24 cm/leaf) occurred at $2\times$ trace elements and the most significant increment in leaf number (4.83 ± 1.01 leaves/plant) occurred at $1\times$ trace elements (Figures 6E–6H). Moreover, the highest contents of chlorophyll *a* (1.82 ± 0.16 mg/g FW), chlorophyll *b* (0.71 ± 0.08 mg/g FW), and total chlorophyll (2.53 ± 0.23 mg/g FW) of *B. gymnorrhiza* occurred at $2\times$ trace elements. The highest contents

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of chlorophyll *a* (1.15 ± 0.04 mg/g FW), chlorophyll *b* (0.45 ± 0.02 mg/g FW), and total chlorophyll (1.60 ± 0.06 mg/g FW) of *A. ilicifolius* occurred at $1 \times$ trace elements (Figure S5 in ESM).

DISCUSSION

Effects of illumination durations and intensities on cultivation of *B. gymnorrhiza* and *A. ilicifolius*.

The light enhanced seed germination in both species. Long illumination durations and high illumination intensities promoted germination of *B. gymnorrhiza*, while short illumination durations promoted germination of *A. ilicifolius*. A previous study found that the effects of light on seed germination are species-specific (Ma et al. 2021). For example, a long illumination duration enhanced the germination rate of *Camellia sinensis* (Hu et al. 2024) but inhibited that of *Panax ginseng* (Lee et al. 2022).

Short illumination duration and appropriate illumination intensity promoted seedling growth in both species. Optimal illumination duration and intensity are crucial for photosynthesis and growth of coastal plants, especially in intertidal and low-tide zones (Lekammudiyanse et al. 2023). Mangrove plants in these areas adapt to tidal changes and limited sunlight. Short illumination duration and appropriate illumination intensity enhance photosynthesis and energy production, supporting their growth (Jiang et al. 2019). However, excessively long illumination duration and high illumination intensity lead to photo-oxidative damage and reduce photosynthetic efficiency (Krause, Winter 2021). For example, tipburn was observed in lettuce ‘Crunchy’ under high illumination intensity of $300 \mu\text{mol}/\text{m}^2/\text{s}$ (Miao et al. 2023).

Effects of salinities and temperatures on the cultivation of *B. gymnorrhiza* and *A. ilicifolius*.

Low salinity promoted seed germination and seedling growth in both species, while high salinity restrained them. Moreover, *A. ilicifolius* was more inhibited by salinity than *B. gymnorrhiza*. A previous study indicated that viviparous mangrove species like *Aegiceras corniculatum* were more salt-tolerant than nonviviparous species like *A. ilicifolius* and *Sonneratia caseolaris* (Wijayasinghe et al. 2019). Moreover, Ye et al. (2005) found that salinity above 25‰ inhibited seed germination and seedling growth of *A. ilicifolius*, *A. corniculatum* and *Avicennia marina*. *Bruguiera parviflora* grew best at 100 mM NaCl (salinity of 5.85‰) but was in-

hibited at higher salinity (Parida et al. 2004). When salinity exceeds the tolerance threshold, it disrupts plant water uptake and nutrient absorption, leading to ionic toxicity (Taghvaei et al. 2022). Additionally, a certain amount of salt supports the growth of mangroves (Patel et al. 2010). A previous study found that *Kandelia obovata* seedlings grew better in saltwater than in freshwater (Zhou et al. 2024).

A warm temperature (28–32 °C) promoted seed germination and seedling growth of both species. As mangrove plants are found only in the tropics and subtropics, this suggests they require higher temperatures to grow. A warm temperature (25–30 °C) promoted the photosynthesis and respiration of mangrove plants, supporting their growth (Inoue et al. 2022). For example, the growth rate of *Rhizophora stylosa* seedlings increased as the temperature rose from 15 °C to 30 °C (Akaji et al. 2019).

Effects of nutrient conditions on the cultivation of *B. gymnorrhiza* and *A. ilicifolius*.

Nutrient addition had little effect on germination of *A. ilicifolius*, but appropriate addition of commercial fertiliser, $\text{Ca}^{2+}/\text{Mg}^{2+}$ and trace elements enhanced germination of *B. gymnorrhiza*. The addition of 0.03 g/kg substrate of Stanley shortened the germination cycle of *B. gymnorrhiza*, suggesting that proper addition of fertiliser improved nutrient uptake of halophytes (Cai et al. 2022). For example, the addition of bio-phosphate fertiliser improved germination of quinoa (Amiryousefi et al. 2022). Moreover, the addition of $2 \times \text{Ca}^{2+}/\text{Mg}^{2+}$ and $0.5 \times$ trace elements promoted germination of *B. gymnorrhiza*. These findings align with those of Wang et al. (2022), who found that water-soluble fertilisers containing $\text{Ca}^{2+}/\text{Mg}^{2+}$ promoted the germination of cucumber. Jia et al. (2021) also found that low concentrations of Fe^{2+} , Mn^{2+} , B^{3+} and Mo^{6+} promoted germination of *Polygala tenuifolia*.

The proper addition of commercial fertiliser, including $\text{Ca}^{2+}/\text{Mg}^{2+}$ and trace elements, promoted seedling growth of both species, while excessive or insufficient addition restrained their growth. Proper nutrient supply promotes plant growth. For example, Yates et al. (2002) found that a balanced supply of nitrogen, phosphorus and potassium enhanced the growth of *A. marina*, *Ceriops tagal* and *R. stylosa*. Moreover, the excessive addition of Stanley inhibited the growth of *B. gymnorrhiza*. As high nitrogen and phosphorus concentrations cause metabolic imbalance, reduce root water and nutrient absorption, and ultimately inhibit growth (Mack et al. 2024). Additionally, the insufficient

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addition of $\text{Ca}^{2+}/\text{Mg}^{2+}$ and trace elements limited the growth of both species. A lack of nutrients directly affects essential physiological processes, such as photosynthesis, cell division, and root development (de Bang et al. 2021).

CONCLUSION

This study optimised seed germination and seedling cultivation conditions for *B. gymnorrhiza* and *A. ilicifolius* in a plant factory. The optimal conditions for seed germination of *B. gymnorrhiza* were an illumination duration of 18 h/day, an illumination intensity of $400 \mu\text{mol}/\text{m}^2/\text{s}$, a salinity of 10‰, a temperature of 28–32 °C, 0.03 g/kg of Stanley commercial fertiliser in the substrate, $2\times \text{Ca}^{2+}/\text{Mg}^{2+}$ and $0.5\times$ trace elements. In comparison, the optimal conditions for *A. ilicifolius* seeds were an illumination duration of 6 h/day, an illumination intensity of $100 \mu\text{mol}/\text{m}^2/\text{s}$, a salinity of 5‰, a temperature of 28–32 °C and 5.39 g/kg of Yuanlv commercial fertiliser in the substrate. For seedling cultivation, *B. gymnorrhiza* grew best under an illumination duration of 8–12 h/day, an illumination intensity of $100 \mu\text{mol}/\text{m}^2/\text{s}$, a salinity of 0–10‰, a temperature of 28–32 °C, 0.53 g/kg of Stanley commercial fertiliser in the substrate, $0.5\times \text{Ca}^{2+}/\text{Mg}^{2+}$ and $2\times$ trace elements. In comparison, the optimal conditions for *A. ilicifolius* seedlings were an illumination duration of 8–12 h/day, an illumination intensity of $200 \mu\text{mol}/\text{m}^2/\text{s}$, a salinity of 0–5‰, a temperature of 28–32 °C, 5.39 g/kg of Yuanlv commercial fertiliser in the substrate, $3\times \text{Ca}^{2+}/\text{Mg}^{2+}$ and $0.5\text{--}2\times$ trace elements. Overall, *B. gymnorrhiza* showed better growth performance than *A. ilicifolius* in plant factories. Our results provide a novel seedling cultivation method that enhances the efficiency of seedling cultivation for both species, with potential applications in the restoration of mangrove forests.

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