

## RESEARCH PAPER

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# Fruiting traits and seedling regeneration of the relict mangrove plant *Nypa fruticans* Wurmb in China

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**Abstract**

*Nypa fruticans* Wurmb is both a relic plant and a true mangrove. In China, wild populations are distributed only on Hainan Island and face significant challenges in regeneration from seedlings. This study explored the underlying causes of recruitment limitation by examining seed morphological traits from three distinct populations (Haikou, Wenchang and Wanning) and analysing seed germination and seedling growth characteristics under varying conditions. The key findings are as follows: fruiting and seed-setting rates for *N. fruticans* were notably low, standing at only 21 and 40%, respectively. The Wanning population exhibited significantly higher rates compared to the other two populations. Under natural conditions, the germination and seedling emergence rates were also modest, at 36.58 and 22.99%, respectively. The germination and emergence rates of the Wanning population were significantly greater than those of the Haikou and Wenchang populations. Meanwhile, seeds from a single population did not differ in germination rates among three *in situ* *N. fruticans* habitats, but seedling emergence rates differed significantly. Optimal conditions for seed germination involved a light intensity of 60%, a salinity of 5‰ and a flooding time of 8 h/day. In natural settings, these three environmental factors fall short of the ideal conditions. The study underscores that light, salinity and flooding are primary factors contributing to the limitations in *N. fruticans* seedling recruitment. In addition to advocating increased investment in scientific research and technology to address seed source issues, we recommend heightened efforts in habitat restoration, *in situ* conservation and the optimization of relocation and field return strategies to bolster *N. fruticans* populations.

**Introduction**

East Asia harbours a diverse range of relic monotypic genera dating back to the Paleozoic, Neogene and even Cretaceous periods (Tang et al., 2018). Presently, some of these genera have degenerated into unique single-species populations that are reduced in size and limited to specific habitats in tropical and subtropical China. Notable examples include *Ginkgo biloba* L., *Metasequoia glyptostroboides* Hu & W. C. Cheng, *Thuja sutchuenensis* Franch, *Taiwania cryptomerioides* Hayata, *Cathaya argyrophylla* Chun et Kuang, and *Nypa fruticans* Wurmb (Tang and Ohsawa, 2002; Tang et al., 2011, 2015; He et al., 2015; Qian et al., 2016; Lovly and Merlee Teresa, 2016). Over the last 50 years, over 200 species have become extinct, and nearly 5000 plant species are currently threatened (Volis, 2016). The decline of these wild plant populations in China during the 20th and 21st centuries is primarily attributed to habitat loss, environmental pollution and global climate change (Xu et al., 2021) and their conservation is essential for biodiversity maintenance (Brown et al., 2015; Qin et al., 2017). In addition to threats from their limited geographic range, small population size and fragile habitats, continuing the decline of such species is exacerbated primarily by low fruit set, seed set, seed germination and seedling survival rates (Neaves et al., 2015). Understanding their life history and how they respond to their environment is, therefore, crucial for their conservation.

Seed germination is a critical phase in the plant life cycle, susceptible to various factors and often a bottleneck for natural regeneration (Jimenez-Alfaro et al., 2016; Jiang et al., 2022). Research has shown that seeds of mangrove plants respond differently to their environment in various habitats (Su et al., 2021). Key indicators of seed germination include initial germination time, germination rate and emergence rate, which are crucial for seed-to-seedling transition and natural regeneration (Rosbakh and Poschlod, 2015). These differences in seed germination traits reflect the adaptation strategies of different species (Li et al., 2020).

Mangroves grow in the intertidal region between land and sea and are affected by a variety of environmental factors such as light, moisture, salinity, tides, temperature, soil and wind (Zhang, 2019). Current studies on the relationship between mangroves and the environment

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have focused on shade tolerance, salt tolerance and flooding tolerance of seedlings (Lv et al., 2019). Therefore, through simulation experiments, the seed germination characteristics of endangered mangrove plants are studied to explore the limiting factors of seedling regeneration, which can provide a basis for elucidating the causes of their endangerment and formulating conservation strategies (Li et al., 2020; Jiang et al., 2022).

Vivipary in plants refers to a phenomenon in which sexually reproduced offspring germinate while still attached to the mother plant (Robert et al., 2015). This is mostly manifested in mangrove plants, which occur in tropical and subtropical intertidal zones and encounter harsh environmental conditions such as high salinity, high temperatures, waterlogging, hypoxia and tidal waves (Zhou et al., 2016). Extensive research has shown that high salt inhibits growth, while low salt promotes it (Liu et al., 2017). Both viviparous and non-viviparous propagules prefer low salt environments, but some require specific salinity for germination (Robert et al., 2015). Viviparous propagules can survive prolonged flooding and benefit from tidal actions (Liu et al., 2022). Excessive flooding affects colonization and survival due to waterlogged soil, which reduces photosynthesis and growth (Yan et al., 2004; Zhou et al., 2023). Light plays a crucial role in propagule colonization. Viviparous propagules with chlorophyll in their epidermis can photosynthesize, while those without cannot (Liu and Liao, 2013). Propagules respond to varying light intensity by adjusting leaf area and chlorophyll content (Ulqodry et al., 2014). Interspecies differences exist in the effect of shading on embryonic axis survival (Duke and Watkinson, 2002). The water column's salinity and pH change continuously, and different mangrove species cope with flooding with varying levels of success (Liu et al., 2022).

*N. fruticans*, a true mangrove plant of the genus *Nypa* in the Areaceae family, thrives in calm estuaries and coastal areas. It is primarily found on the landward side of mangrove forests in low salinity areas (Zakaria et al., 2017). *N. fruticans* is an ecologically and economically vital component of East Asian mangrove ecosystems (Lovly and Merlee Teresa, 2016). Climate change and human activities have drastically reduced its global distribution (Jian et al., 2010). Currently, its natural range is restricted to the paleotropics (India-Australia), and in China, it is naturally distributed only on Hainan Island (Zhang et al., 2022). Field surveys revealed that there are only four natural populations of *N. fruticans* in China, which are naturally distributed in Haikou, Wenchang, Qionghai and Wanning on Hainan Island. Only the Wanning population showed a cluster distribution in patches, while other populations were scattered. *N. fruticans* is a protected species and is listed in the Red Book of Chinese Plants, with its protection status upgraded from national level 3 to level 2 in 2021 (Fu, 1991; Zhang et al., 2023).

Previous research on the reproductive characteristics of *N. fruticans* has revealed that it has a low fruit set rate of 37.58% and low germination rates of 1.85% (Rozainah and Aslezaeim, 2010). Through the preliminary investigation, there were very few seedlings under the *N. fruticans* forest in China, indicating that there were serious seedling regeneration restrictions. However, the potential causes for this phenomenon are not clear. At present, there are few studies on the adaptability of *N. fruticans* seeds, so it is necessary to obtain their responses to environmental factors such as light, salinity and flooding time through single-factor gradient experiments, which will provide basic data for the in-depth study of their environmental adaptation mechanisms.

Therefore, we hypothesized that seed germination and seedling regeneration of *N. fruticans* are related to environmental factors and tested this hypothesis by (i) comparing fruit and seed traits of different *N. fruticans* populations, (ii) comparing seed germination characteristics of different *N. fruticans* populations and germination characteristics of seeds from a single population in multiple *in situ* *N. fruticans* habitats and (iii) exploring the effects of different environmental factors (light intensity, salinity and flooding time) on *N. fruticans* seed germination.

## Materials and methods

### Materials

*N. fruticans* is a tufted evergreen shrub that grows a height of 3–9 m. The rhizome is creeping and grows horizontally in the sea-shore mud. The infructescence is capitate, containing 32–38 mature carpels. Each small fruit develops from one carpel. Mature carpels are drupe-like, brown, shiny, obovate, 9–11 cm long, slightly compressed and hexagonal. Each small fruit contains one seed, which is round and measures about 3–4 cm long and 4 cm wide. *N. fruticans* has fruit all year round, but most fruit is produced in June and July.

Through preliminary field surveys, we found that there were four natural populations of *N. fruticans* plants on Hainan Island, with the population number being about 9319 trees (Table 1). Of these, seedlings were found in the understory of all populations, except the Qionghai population. Therefore, three natural populations of *N. fruticans* (Haikou, Wenchang and Wanning) were selected for the study.

In order to obtain sufficient seeds, 50 healthy plants were randomly selected as sampling mother trees and tagged at each of the three *N. fruticans* populations before the start of the experiment. To prevent the seeds from falling and being washed away by seawater, netting was placed over the infructescence and secured before ripening. When the infructescence was ripe and split, the netting was then transported back to the laboratory along with the infructescence.

### Methods

#### Fruiting traits of *N. fruticans* from different populations

Before flowering, 100 trees of *N. fruticans* were randomly labelled from each population. After infructescence ripening, the natural fruit set rate was calculated for each population and repeated three times. Fruit set refers to the percentage of the total number of flowers in the tree that actually set fruit in the natural state. Twenty-five infructescences were randomly selected from each population and the infructescence diameter was measured with a tape measure. After infructescence dehiscence, the seed set rate of each infructescence was calculated. The seed set rate refers to the number of full seeds as a percentage of the total number of seeds. The maximum longitudinal length and the maximum transverse length of each fruitlet were measured with vernier calipers (Li et al., 2020; Jiang et al., 2022).

#### Germination characteristics of *N. fruticans* seeds under natural environmental conditions

(1) Germination characteristics of seeds from different populations under the common garden experiment

**Table 1** Geographic distribution and resource status of *N. fruticans*

Populations	Geographical coordinates	Population number	Tide time (h/day)	Salinity (‰)	Canopy density (%)
Haikou	110°35'27.00"E; 19°57'04.90"N	161	10–14	22.31–24.52	80–90
Wenchang	110°48'18.93"E; 19°37'11.32"N	80	9–12	13.79–15.66	60–70
Qionghai	110°40'00.93"E; 19°21'02.62"N	68	8–10	17.12–20.55	50–60
Wanning	110°11'01.90"E; 18°35'42.78"N	9010	10–14	20.82–28.61	70–80

A common garden was constructed in Lingao County, Hainan Province, where there is a mangrove nursery of the Forestry Academy of Hainan Province. From April 2021 to June 2021, 20 infructescences were randomly selected from the Haikou, Wenchang and Wanning populations, respectively. The infructescences were ripe and cracked, and all seeds were packed into seedling bags (Glorious Yi Brand, Shandong Jianyang Biotechnology Co.) with nutrient-rich soil (Stanley Brand, Stanley Agricultural Group Inc.). The seedling bags were divided into three groups according to different populations and placed under the common garden experiment. The experiment was replicated three times. Seed germination rates and emergence rates of seedlings from different populations were counted after 1 and 3 months, respectively.

(2) Germination characteristics of seeds from a single population in three *in situ* *N. fruticans* habitats

From April 2021 to June 2021, 30 infructescences were randomly selected from the Wanning population. Each infructescence was covered with 1 net pocket, totalling 30 net pockets (Summer Snow Brand, Qingdao Summer Snow Fishing Tackle Co.). All net pockets were equally divided into three groups and fixed on mother trees in the natural habitat of *N. fruticans* in Haikou, Wenchang and Wanning, respectively. The experiment was replicated three times. Seed germination rates and emergence rates of seedlings from different populations were counted after 1 and 3 months, respectively.

*Effect of different environmental factors on the seed germination of N. fruticans*

Six hundred and ninety full and pest-free *N. fruticans* seeds were randomly selected from the Wanning population and inserted into culture bags filled with sandy soil. Four light intensity treatment groups, 8 salinity treatment groups and 11 flooding treatment groups were designed, and single-factor experiments for light, salinity and flooding were established separately (Table 2). Different light intensity treatment levels were adjusted using shade nets (Lvandi, Greenland Shade Co.) with different shading effects. Salinity manipulations were carried out using sea salt (from Dongfang City Saltwork) and tap water. Salinity levels were checked and adjusted weekly. To reflect semi-diurnal tides, watering was divided into two injection/discharge cycles per day (Table 3). The flooding and draining for each group were controlled with mini water pumps (Type: HQB – 2000, rated power: 24 W, pump head: 1.8 m and pump flow: 1400 L/h). Each group had 30 seeds (10 seeds per treatment in 3 replications). The experiment was conducted from March 2022 to June 2022, and the test site was located in the mangrove nursery base of the Hainan Academy of Forestry (Hainan Academy of Mangrove).

*Data analysis*

Six indices were selected to measure fruiting traits: infructescence diameter, number of small fruits per infructescence, maximum longitudinal length, maximum transverse length, fruit setting rate and seed-setting rate. Eight indices were selected to measure seed germination characteristics: initial germination time, germination duration, germination rate, initial emergence time, emergence duration, emergence rate, seedling height and number of leaves. The criterion for germination was the protrusion of the terminal bud from the pericarp, and the absence of germination of the embryonic axis for five consecutive days marked the end of the germination experiment. Meanwhile, the criterion for seedling emergence was the emergence of the first pair of leaves from the terminal bud, and the absence of seedling emergence for five consecutive days marked the end of the seedling emergence experiment.

Initial germination time was the length of time from the beginning of the germination test to the first germination event. Initial emergence time was defined as the length of time from the beginning of the germination test to the first seedling emergence. Germination duration was the length of time from the first germination event to the end of the germination test, and emergence duration was the length of time from the first seedling emergence to the end of the seedling emergence test. The germination (GP) and emergence rates (SR) were calculated as follows:

$$GP = \frac{Ga}{Gn} \times 100\%; \quad SR = \frac{Ns}{Na} \times 100\%$$

In the above equation, *Ga* represents the number of seeds that have germinated, *Gn* represents the number of seeds supplied for testing, and *Ns* represents the final number of seedlings that survived.

The mean and standard error (*SE*) of three replicates were calculated. Data on all measurement indicators were analysed for the differences among different treatments by the analysis of variance. If the difference was significant at  $P < 0.05$ , a Duncan test was employed to determine the potential source of the difference. All statistical analyses were performed with SPSS, version 16.0 (SPSS Inc., Chicago, IL, USA). Statistical significance was defined as  $P < 0.05$ .

**Results**

*Fruiting traits of N. fruticans from different populations*

The diameter and number of fruitlets per *N. fruticans* infructescence were  $26.49 \pm 2.13$  cm and  $82.16 \pm 4.22$ , respectively. The infructescence diameter and number of small fruits from Wanning were significantly greater than those from Haikou and Wenchang. The maximum longitudinal length and the maximum

**Table 2** Experimental design for the germination of *N. fruticans* seeds

Factors	Treatment groups	Light intensity treatments (%)	Salinity treatments (%)	Flooding time treatments (h/day)
Light intensity	1	20	5	4
	2	40	5	4
	3	60	5	4
	4	100	5	4
Salinity	1	60	0	4
	2	60	5	4
	3	60	10	4
	4	60	15	4
	5	60	20	4
	6	60	25	4
	7	60	30	4
	8	60	35	4
Flooding time	1	60	5	2
	2	60	5	4
	3	60	5	6
	4	60	5	8
	5	60	5	10
	6	60	5	12
	7	60	5	14
	8	60	5	16
	9	60	5	18
	10	60	5	20
	11	60	5	22

transverse length of small fruits were  $9.59 \pm 0.11$  cm and  $7.19 \pm 0.14$  cm, respectively, and the differences in the maximum longitudinal length and the maximum transverse length among the various populations were not significant. In addition, the natural fruiting and seed-setting rates were only  $21.11 \pm 8.75$  and  $40.40 \pm 5.31\%$ , respectively, with the fruiting and seed-setting rates from

Wanning also being significantly higher than those from Haikou and Wenchang (Table 4).

#### Germination characteristics of *N. fruticans* seeds under the natural environment

Under the same common garden conditions, the differences in germination and seedling emergence rates among the three populations were highly significant. The germination and emergence rates of the Wanning population were significantly greater than those of the Haikou and Wenchang populations, and the order of germination rates and emergence rates among the various populations was Wanning > Wenchang > Haikou. Mean values of germination and seedling emergence rates were  $36.58 \pm 5.16$  and  $22.99 \pm 3.74\%$ , respectively (Fig. 1A). Under different common garden experiments, the germination rate of seeds from the same population did not differ significantly among three *in situ* habitats, though interestingly the emergence rate differed significantly. The seedling emergence rate in the Wanning habitat was significantly higher than that in the remaining two habitats (Fig. 1B).

#### Effect of light intensity on *N. fruticans* seed germination

Under different light intensity treatments, the initial germination time, germination duration and germination rate of *N. fruticans*

**Table 3** Time of injection and discharge of water per day

Flooding time (h)	Injection water time	Discharge water time
2	0:00; 12:00	1:00; 13:00
4	0:00; 12:00	2:00; 14:00
6	0:00; 12:00	3:00; 15:00
8	0:00; 12:00	4:00; 16:00
10	0:00; 12:00	5:00; 17:00
12	0:00; 12:00	6:00; 18:00
14	0:00; 12:00	7:00; 19:00
16	0:00; 12:00	8:00; 20:00
18	0:00; 12:00	9:00; 21:00
20	0:00; 12:00	10:00; 22:00
22	0:00; 12:00	11:00; 23:00



**Table 4** Fruiting traits of *N. fruticans* from different populations

Seed traits	Haikou	Wenchang	Waning	Mean $\pm$ standard deviation
Infructescence diameter (cm)	24.48 $\pm$ 4.24b	25.55 $\pm$ 4.63b	29.44 $\pm$ 2.16a	26.49 $\pm$ 2.13
Number of small fruits per infructescence	77.71 $\pm$ 16.63b	80.95 $\pm$ 16.70ab	87.82 $\pm$ 17.27a	82.16 $\pm$ 4.22
Maximum longitudinal length (cm)	9.55 $\pm$ 0.81a	9.49 $\pm$ 0.88a	9.74 $\pm$ 0.80a	9.59 $\pm$ 0.11
Maximum transverse length (cm)	7.06 $\pm$ 0.84a	7.13 $\pm$ 0.80a	7.39 $\pm$ 0.68a	7.19 $\pm$ 0.14
Fruit setting rate (%)	13.33 $\pm$ 2.36b	16.67 $\pm$ 4.71b	33.33 $\pm$ 4.71a	21.11 $\pm$ 8.75
Seed-setting rates (%)	35.98 $\pm$ 5.16b	37.36 $\pm$ 6.93b	47.87 $\pm$ 7.88a	40.40 $\pm$ 5.31

Different letters indicate a significant difference ( $P < 0.05$ ).

seeds were not significantly different ( $p > 0.05$ ), though the initial emergence time, emergence duration, emergence rate, seedling height and number of leaves did differ among groups ( $p < 0.05$ ).

All treatment groups started germination on the first day of the experiment and lasted for about 3 days. With increasing light intensity, the initial emergence time and emergence duration first decreased then increased, with minimum values of 6.33 and 8 days at 60% and maximum values of 9.67 and 13.33 days at 100% of light intensity, respectively (Fig. 2A). The germination rate and seedling emergence rate showed a trend of increasing and then decreasing, where the germination rate remained above 70% among all light treatments, and the seedling emergence rate had a maximum value of 70% at 60% light intensity, and the emergence rate (50%) under full light conditions was significantly smaller than the remaining three treatments (Fig. 2B). Seedling height showed a trend of increasing and then decreasing, with a maximum value of 34.53 cm at 60% light intensity and a minimum value of 21.75 cm at 100% (Fig. 2C). The number of leaves tended to decrease gradually, with a maximum value of 4.25 leaves at 20% light intensity and a minimum value of 1.75 leaves at 100% (Fig. 2D).

#### Effect of salinity on *N. fruticans* seed germination

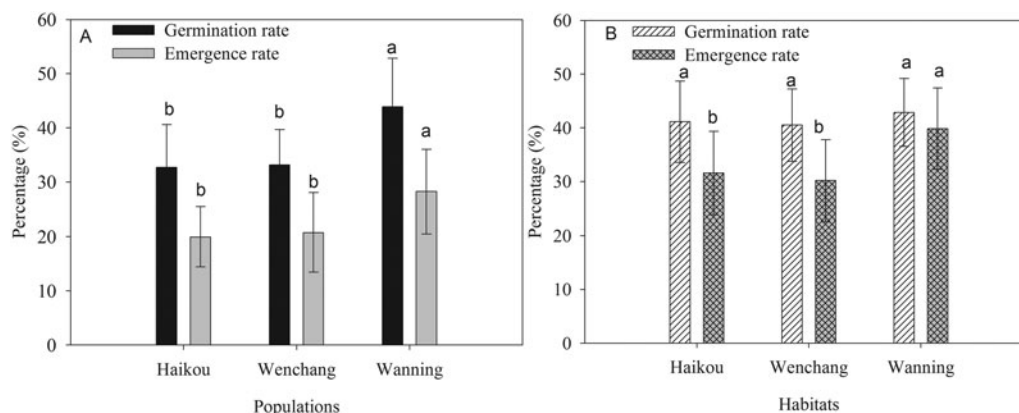
All germination indicators of *N. fruticans* seeds were significantly different under different salinity treatments ( $P < 0.05$ ). Each indicator gradually increased in the salinity range of 0–20‰, and the initial germination time, germination duration, initial emergence time and emergence duration increased by 12, 19, 24 and 26 days in a 20‰ saline solution compared with the control (Fig. 3A).

In the salinity range of 0–25‰, both germination and emergence rates first increased, then decreased among treatments, with maximum values of 63.33 and 50% at 5‰, respectively. In the salinity range of 5–25‰, these two indicators among treatments were significantly lower than those in the salinity range of 0–5‰. The germination rate and seedling emergence rate were 0 at salinities above 25‰ (Fig. 3B). Both seedling height and leaf number showed a trend of increasing and then decreasing, with maximum values at salinities of 5 and 10‰, respectively. Seedling height and leaf number under salinities of 0–10‰ were significantly greater than those under 10–20‰ (Figs. 3C and 3D).

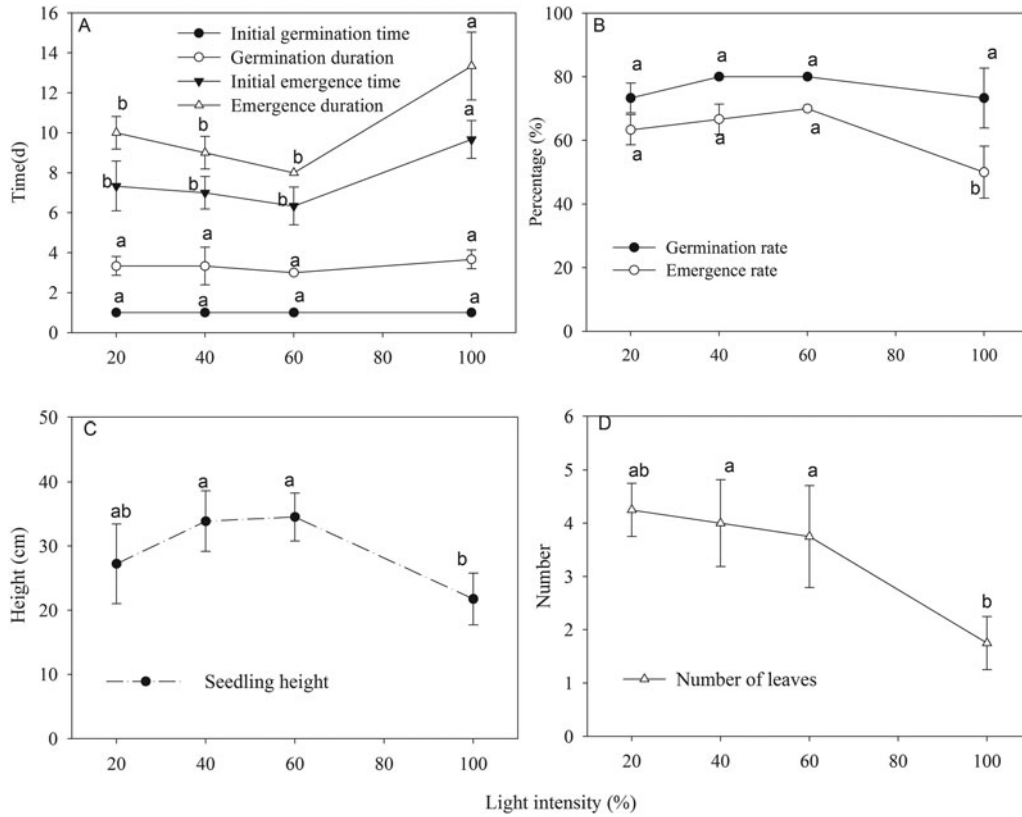
#### Effect of flooding time on *N. fruticans* seed germination

Under different flooding treatments, the germination indicators of *N. fruticans* seeds were significantly different, with the exception of initial germination time ( $P < 0.05$ ). All treatment groups started germination on the first day. With the increase of flooding time, the germination duration, initial emergence time and emergence duration first decreased, then increased. They all yielded minimum values under the conditions of 8 h/day, then they rose significantly up to maximum values under 22 h/day. The germination duration, initial emergence time and emergence duration were not significantly different among treatments under the conditions of 2–10 h/day flooding time and were significantly lower than those under the conditions of 12–22 h/day (Fig. 4A).

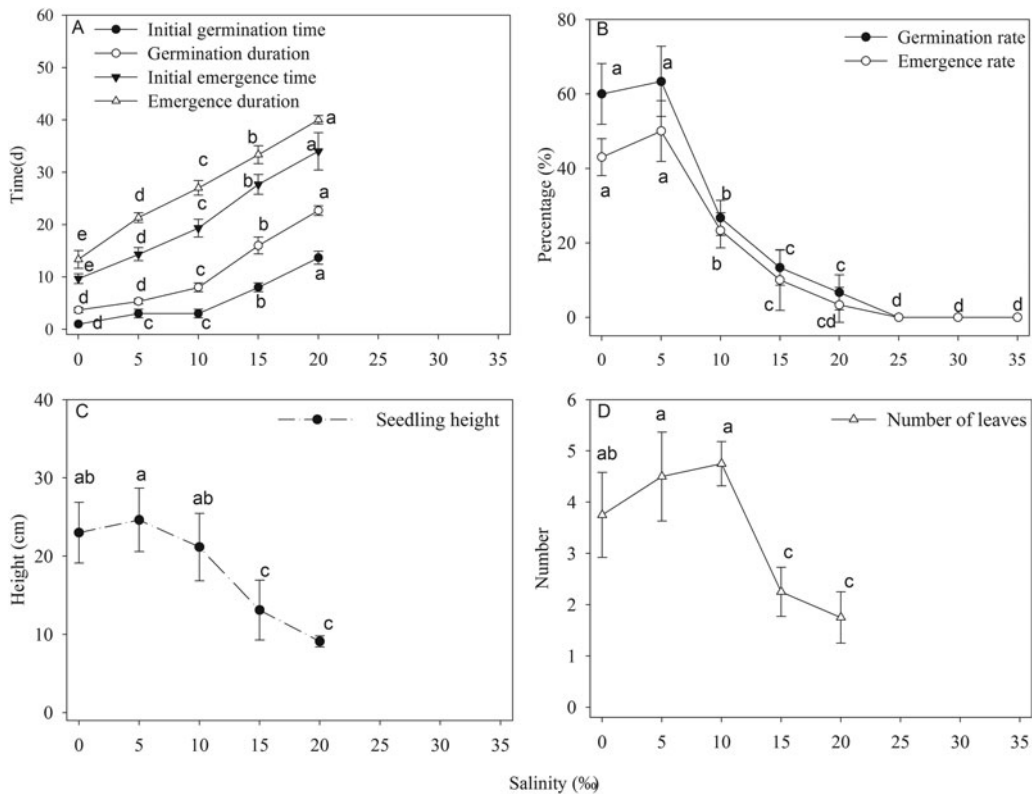
The germination and emergence rates gradually increased among treatments at flooding times of 2–8 h/day, where the germination rate of all treatments had maximum values at 8 h/day, while the emergence rate had a maximum at both 6 and



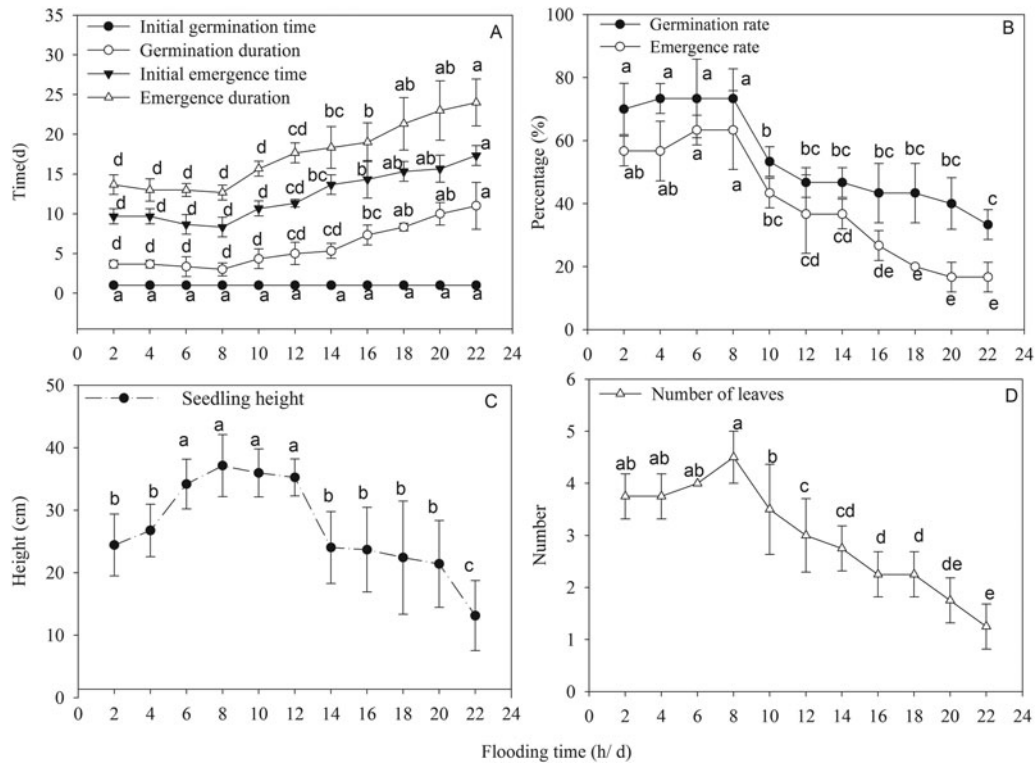
**Figure 1.** Germination characteristics of *N. fruticans* seeds in the natural environment. Different letters indicate a significant difference ( $P < 0.05$ ).



**Figure 2.** Effect of light intensity on *N. fruticans* seed germination. Different letters indicate a significant difference ( $P < 0.05$ ).



**Figure 3.** Effect of salinity on *N. fruticans* seed germination. Different letters indicate a significant difference ( $P < 0.05$ ).



**Figure 4.** Effect of flooding time on *N. fruticans* seed germination. Different letters indicate a significant difference ( $P < 0.05$ ).

8 h/day. The germination rate and seedling emergence rate gradually decreased among treatments at 8–22 h/day and were significantly lower than those at 2–8 h/day (Fig. 4B). Both seedling height and leaf number showed an increasing trend followed by a decreasing trend, with both reaching a maximum at 8 h/day. Seedling height was significantly greater under 6–12 h/day than the rest of the treatment groups, and leaf number was significantly greater under 2–8 h/day than under 10–22 h/day (Figs. 4C and 4D).

## Discussion

### Fruiting traits of *N. fruticans* in China under natural conditions

Fruiting rates, seed-setting rates, germination rates and seedling survival rates are crucial factors in determining the life history and population renewal of plants. Fruit and seed-setting rates are closely linked to plant mating patterns and pollination efficiency (Yang et al., 2020). In our study, we observed that the fruiting and seed-setting rates of *N. fruticans* were relatively low, a phenomenon shared with other endangered plants like *Rhododendron changii* (Fang) Fang and *Sonneratia × hainanensis* W. C. Ko & al. These low rates might be attributed to *N. fruticans*' limited reproductive capabilities (Pluntz et al., 2018; Zhang et al., 2019). Research indicates that *N. fruticans* predominantly relies on outcrossing for sexual reproduction; however, it also exhibits some selfing tendencies (Mantiquilla et al., 2015). Moreover, the flowering period exhibits dichogamy, where pistils mature before stamens. This temporal mismatch, combined with factors like short pollination windows and weather-related disruptions, hampers the successful pollination and seed development of *N. fruticans*, significantly affecting its reproduction (Valdes et al., 2021).

For plant populations, a potential result of habitat fragmentation is the disruption of pollination systems, causing a decline in

reproductive success as small populations become less attractive to pollinators (Winter et al., 2008). Similar studies such as single-plant seed production of *Sanicula europaea* L. decreased when populations were reduced (Kolb and Lindhorst, 2006). Fruit set was significantly lower in small populations of *Catsetum viridiflavum* Hook than in large populations (Donaldson et al., 2010). In the present study, the Wanning population exhibited significantly higher rates of fruiting and seed-setting rates compared to the other two populations. This may be related to its heterogamous pollination and population size. Pollinating insects play an important role in the reproductive process of *N. fruticans* populations (Valdes et al., 2021). Smaller populations will be less attractive to pollinators and their reproductive outputs will be lower compared to larger populations (Su et al., 2021; Jiang et al., 2022). Our field surveys confirmed this, with the Wanning population being the largest, with over 2000 plants, while Haikou and Wenchang populations each contained fewer than 200 plants. This underscores the impact of population size on *N. fruticans*' population renewal. The large-scale decline in *N. fruticans* populations can be attributed to extreme climatic conditions and human activities (Zhang et al., 2022). Studies reveal that *N. fruticans*, once distributed across a wide range, now survive only in the paleotropics due to the extreme climates triggered by Quaternary glaciations (Chen, 2016). During this period, *N. fruticans* populations substantially declined, leading to a loss of genetic diversity. Additionally, *N. fruticans* is a widely utilized mangrove species, subjected to overharvesting and long-term exploitation. The construction of reclamation projects, mariculture bases and real estate developments can result in the extensive destruction of *N. fruticans* populations (Jian et al., 2010).

Seed germination under natural conditions is influenced by factors such as geography, climatic factors and genetic differences

(Sudrajat, 2016). Influenced by geography, the same tree species in different regions produce rich genetic variation due to geography, and this is reflected in seed germination characteristics through stable genetic material (Hao et al., 2021). Previous studies have shown that seed germination and germination speed of *Pinus tabuliformis* Carrière vary greatly in different regions, which may be caused by genetic factors or due to environmental influence (Wang et al., 2015). The high variability in seed germination traits exhibited by *Cercidiphyllum japonicum* Siebold & Zucc was a result of a combination of their own attributes, habitat characteristics and geographic isolation (Li et al., 2020). In this study, the germination and seedling emergence rates of the Wanning population were significantly higher than those of the Haikou and Wenchang populations, which indicated that there were significant population differences in seed germination traits of *N. fruticans*. The reason may be that the long-term growth and reproduction of different *N. fruticans* populations in localized environments may contribute to the genetic differentiation of these populations, which ultimately leads to differences in seed germination and seedling growth characteristics among different populations. We also found that the germination rate of seeds from the same population did not differ significantly among three *in situ* habitats, though interestingly the emergence rate differed significantly. The seedling emergence rate in the Wanning habitat was significantly higher than that in the remaining two habitats. This suggests that the differences in germination characteristics among *N. fruticans* populations may be due to genetic variation among populations and are also influenced by seed source geography and habitat factors.

#### Effect of light intensity on *N. fruticans* seed germination

Plant species exhibit varying requirements for light during seed germination, with effects ranging from promotion to inhibition or no significant impact. Some seeds are highly light-sensitive and necessitate light for germination (Liu et al., 2016; Zhang et al., 2019). Under darkness and constant temperature, the newly collected seeds of *S. × hainanensis* and *S. ovata* Backer did not completely germinate, and increased light promoted seed germination and radicle growth. Exposing the seeds to light for 12 h/day is optimal for their seed germination (Zhang et al., 2019; Ren et al., 2021). Likewise, there were significant differences in the germination rates of *Bruguiera gymnorhiza* and *Bruguiera sexangula* (Lour.) Poir. seeds under different conditions of shading intensity (Zhang et al., 2019). In our study, we experimented with different light gradients by employing artificial shading to observe *N. fruticans* seed germination. Surprisingly, we found no significant difference in the initial germination time, germination duration and germination rate of *N. fruticans* seeds under different light intensities. This behaviour can be attributed to the nature of *N. fruticans* seeds. Unlike most plant seeds, *N. fruticans* seeds complete their germination while still attached to the parent tree (Su et al., 2021; Jiang et al., 2022; Zhang et al., 2022). The phenomenon of vivipary is the most common in the plant kingdom with mangrove plants, which can be divided into vivipary and cryptovivipary (Robert et al., 2015). In the former, the embryonic axis extends beyond the pericarp and gradually grows into a columnar seedling. Hence, this type of propagule is often called an embryonic axis (Zhou et al., 2016). Mangrove plants such as *B. gymnorhiza* and *B. sexangula* belong to this type. In the latter, the embryonic axis only breaks through the seed coat but remains enclosed within the fruit.

Cryptoparasitic plants include mangrove plants such as *N. fruticans* and *Aegiceras corniculatum* (L.) Blanco (Yan et al., 2004). In this case, light has less effect on seed germination in *N. fruticans*.

Under natural conditions, not all seeds have the same fate after leaving the parent tree (Liu et al., 2019). The transition from seeds to seedlings is further subjected to rigorous environmental sieves, leading to only a rare seedling surviving to achieve natural renewal (Han et al., 2021). Our study revealed that seedling emergence rates and seedling height in *N. fruticans* tended to increase up to a certain point and then decrease as light intensity varied. The highest values were observed at 60% light intensity, while full light conditions yielded the lowest values. This implies that moderate shading is optimal for *N. fruticans* seedling growth, with both high and low light conditions being unfavourable. Observations in the field also confirm that *N. fruticans* seedlings mainly thrive in the forest understory, making light a key factor affecting seedling regeneration.

#### Effect of salinity on *N. fruticans* seed germination

The seed germination stage is particularly sensitive to salt stress (Zhang et al., 2019). Mangrove plants, specialized in growing in saline environments, require a certain level of salt throughout their life cycle. While they can endure freshwater or low salinity conditions, high salt levels hinder their growth (Lv et al., 2019). Our results indicate that increasing salinity significantly prolonged the initial germination time, germination duration, initial emergence time and emergence duration of *N. fruticans* seeds. At low salinity (5‰), the germination rate, seedling emergence rate, plant height and leaf number were not significantly different from the control (0‰), indicating that low salt concentrations had little effect on *N. fruticans* seed germination. However, as salinity increased, these indicators decreased significantly. When salt concentrations exceeded 25‰, the *N. fruticans* seed germination rate dropped to zero. This phenomenon could be attributed to osmotic effects and ion toxicity caused by high salinity. Osmotic effects inhibit water uptake by seeds, while ion toxicity inhibits cell growth and division (Orlovsky et al., 2016; Saberali and Moradi, 2019). This low salt-promoted, high salt-inhibited behaviour is also observed during seed germination in other mangrove non-viviparous plants like *S. × hainanensis* and *S. ovata*, which display an optimal salinity of 2.5‰ (Zhang et al., 2019; Ren et al., 2021). In contrast, certain viviparous plants, such as *B. gymnorhiza* and *Rhizophora stylosa*, exhibit seed germination suitable for moderate (10‰) and high (20‰) salinity conditions, respectively (Mo et al., 2001). *N. fruticans* falls between non-viviparous and viviparous plants, with an optimum salinity of 5‰. Notably, in the natural habitat, the seawater salinity of *N. fruticans* exceeds 15‰, demonstrating that the salinity in its native environment far exceeds the requirements for *N. fruticans* seed germination. Therefore, salinity simulation experiments confirmed that salinity acts as a limiting factor for both seed germination and seedling regeneration in *N. fruticans*.

#### Effect of flooding time on *N. fruticans* seed germination

Tides are a crucial environmental factor affecting mangrove plant growth, primarily influencing seed dispersal and distribution. Different types of seeds respond differently to tidal influences (Zhang, 2018). As a true mangrove plant, *N. fruticans* is also affected by tidal levels (Zhang et al., 2022). Generally, mangrove



seedlings are submerged in a fully submerged state during most of the tidal cycle. Prolonged inundation time and greater inundation depth during high tides are key factors contributing to low seedling survival rates (Liu et al., 2022).

Numerous studies have shown that the appropriate duration of flooding facilitates the germination of mangrove plant seeds, but prolonged flooding results in slow or even no seed germination (Chen et al., 2006; Liu et al., 2017, 2022). In our study, we observed no significant difference in the initial germination time, germination duration, initial emergence time and emergence duration of *N. fruticans* seeds when flooding time was less than 10 h/day. However, when inundation exceeded 10 h/day, these time indicators significantly lengthened, and germination and emergence rates declined substantially. The most favourable conditions were observed at 8 h/day of inundation. This suggests that 8 h/day is the optimal flooding time for *N. fruticans* seed germination, and 10 h/day acts as a critical threshold. Beyond this threshold, seed germination and seedling establishment are significantly inhibited. The main reason for this phenomenon is that propagules undergo anaerobic respiration under prolonged water immersion, producing and accumulating alcohol, which leads to cellular toxicity (Zhang et al., 2011; Liu et al., 2022). Our field monitoring found that the daily tidal cycle in the natural habitat of *N. fruticans* exceeded 8 h/day. In addition, other scholars' field investigations found that out of 162 *N. fruticans* seedlings, only three seedlings eventually grew into young trees, while most of the seedlings were washed away at high tide. This suggests that the flooding time dynamic plays a crucial role in the life cycle of *N. fruticans*.

### Conservation strategies for natural populations of the endangered plant *N. fruticans*

To protect the genetic diversity of the endangered mangrove plant *N. fruticans* and foster natural renewal and population expansion, we propose the following conservation strategies in response to the factors contributing to its endangerment.

First, we suggest increasing investment in scientific research and technology to address seed source problems and expand population size. This involves several key initiatives:

1. Employing assisted pollination techniques, bagging tests and pollen cryopreservation to mitigate pollen limitations and low seed germination rates caused by overlapping flowering periods.
2. Utilizing traditional selection and molecular breeding methods, incorporating both asexual and sexual approaches, to develop efficient breeding techniques for *N. fruticans*, thereby increasing the number of high-quality populations.
3. Introducing *N. fruticans* germplasm resources from populations with high genetic diversity, while considering the potential for genetic contamination, to enhance the genetic diversity and germplasm sources. This should be complemented by establishing a *N. fruticans* germplasm nursery to produce high-quality seedlings at the scale.

Secondly, enhancing habitat restoration and *in situ* protection is vital to create a suitable ecological environment. This involves taking the following actions:

1. Implementing measures such as tree species transformation, pest control, tidal ditch restoration and light beach restoration

to rehabilitate degraded *N. fruticans* habitats, enabling natural population renewal.

2. Designating key protection areas within *N. fruticans* habitats to prevent disturbances from human activities through regular patrolling. Utilizing nets over fruit-bearing *N. fruticans* and fencing under the *N. fruticans* forest to reduce the destructive effects of tides on seeds, further enhancing the plant's natural renewal capabilities.
3. In cases where *N. fruticans* populations are small within *in situ* conservation areas, transplanting numerous seedlings from established resource beds to replace degraded populations can be employed while adjusting stand density for improved restoration and protection effects.

Finally, we recommend optimizing relocation protection and field return strategies, followed by continuous monitoring and post-care. These measures should be carried out as follows:

1. Identify suitable relocation sites by conducting detailed assessments of ecological factors, such as climate, tide patterns, soil quality, vegetation and benthic organisms within *N. fruticans*' current habitat, combined with the necessary conditions for seed germination and seedling growth.
2. Domesticating seedlings in the field, after they meet release criteria from the nursery, involves continuous environmental monitoring and adjustments to reduce the impact of endangerment factors and enhance seedling survival rates.
3. Introduce a significant number of *N. fruticans* seedlings into natural or semi-natural habitats suitable for their distribution through artificial propagation. This will help establish new populations with sufficient genetic resources to adapt to evolving conditions and sustain natural renewal.

### Conclusion

In summary, our analysis of *N. fruticans*' seed traits and germination characteristics under natural conditions has led us to conclude that there is a significant limitation in seedling regeneration. This limitation was confirmed through controlled environmental experiments, where we identified light, salinity and flooding as the primary factors constraining seedling regeneration. These findings have significant implications for the preservation and restoration of *N. fruticans* populations. Based on these observations, we recommend a comprehensive approach to conserve and recover *N. fruticans* populations, with a focus on scientific research and technology, habitat restoration, *in situ* protection, relocation and continuous monitoring. These strategies are vital for the self-renewal of this endangered mangrove plant and the expansion of its population size.

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