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PRIMARY RESEARCH PAPER

# Adaptive phenotypic plasticity of *Avicennia officinalis* L. across the salinity gradient in the Sundarbans of Bangladesh

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**Abstract** Adaptive phenotypic plasticity of *Avicennia officinalis* across the salinity gradient in the Sundarbans of Bangladesh was studied. Propagule morphology was compared through use of a completely randomized design. Propagule growth initiation traits across the salinity gradient (from 0 to 35 ppt at 5 ppt interval) were studied by means of a randomized block design. Propagules showed variability in length, width, and weight across the salinity gradient in the Sundarbans. Propagule growth initiation time, mean growth initiation time, growth initiation index, and propagule growth initiation percentage of *A. officinalis* varied significantly with the increasing salinity and among low, medium, and high saline zones. However, propagules originating from the high and medium saline zones started their growth initiation more rapidly and vigorously at high salinities compared to those from the low saline zone. Therefore, *A. officinalis* exhibited adaptive phenotypic plasticity in terms of variability in propagule size and weight as well as physiologically adaptive plastic responses during propagule growth initiation across the salinity gradient in the Sundarbans. *A. officinalis* in high and medium saline zones of Sundarbans is the most salt-adapted phenotype, and a good knowledge about this will be widely useful for successful regeneration, coastal afforestation, and conservation of this species in increasing saline environments in the future.

**Keywords** Mangrove · Morphological · Physiological · Plastic response · Propagule growth initiation · Propagule origin

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## Introduction

Mangroves are the halophytic plants (Waisel, 1972) which grow in the intertidal zones (Lear & Turner, 1977) of the tropical and subtropical coastlines, and provide protection to the coastal dwellers against tropical cyclones and tidal surges (FAO, 1994). For instance, Sundarbans, the world's largest coastal wetland (Gopal & Chauhan, 2006) and the single largest tract (6017 $km^2$) of natural mangrove forest, situated in the south-west corner of Bangladesh

(21°30′–22°30′N, 89°00′–89°55′E) (Iftekhar & Saenger, 2008; Minar et al., 2013) (Fig. 1), protects the vulnerable coastal regions of the country against frequently occurring natural disasters such as tropical storms, tidal surges, wave energy, soil erosion, and salt intrusion from the Bay of Bengal (Rahman & Biswas, 2011). Considering the protective roles of the Sundarbans, the Bangladesh Forest Department initiated coastal afforestation with mangrove tree species in the coastal regions in 1966 in order to protect the coastal people from such natural calamities (Das & Siddiqi, 1985). Now, the area of these mangrove plantations extends approximately up to 200,000 ha (Papry, 2014).

The distribution, development, and establishment of mangrove forests in the estuarine environments are greatly influenced by the environmental factors such as tidal inundation, rate of sedimentation, and salinity. The propagules of mangroves are naturally exposed to the fluctuations of these abiotic factors at the soil surface. Tidal inundation distributes sediment, nutrients, and propagules. The high rate of sedimentation influences soil accretion, soil aeration, nutrient availability, and even buries slow-growing propagules (Tomlinson, 1986; Hutchings & Saenger, 1987). Specifically, salinity is the most critical environmental factor which regulates mangrove plant species distribution, propagule viability, germination, growth initiation, early development, dominance, reproduction, morphology, colonization, and zonation in the coastal environments (Waisel, 1972; Cavalcanti et al., 2007; Janousek & Folger, 2013; Chen & Ye, 2014; Mahmood et al., 2014; Urrego et al., 2014). For example, based on the level of salinity, the Sundarbans is divided into low saline zone (LSZ) in the eastern part, medium saline zone (MSZ) in the central part, and

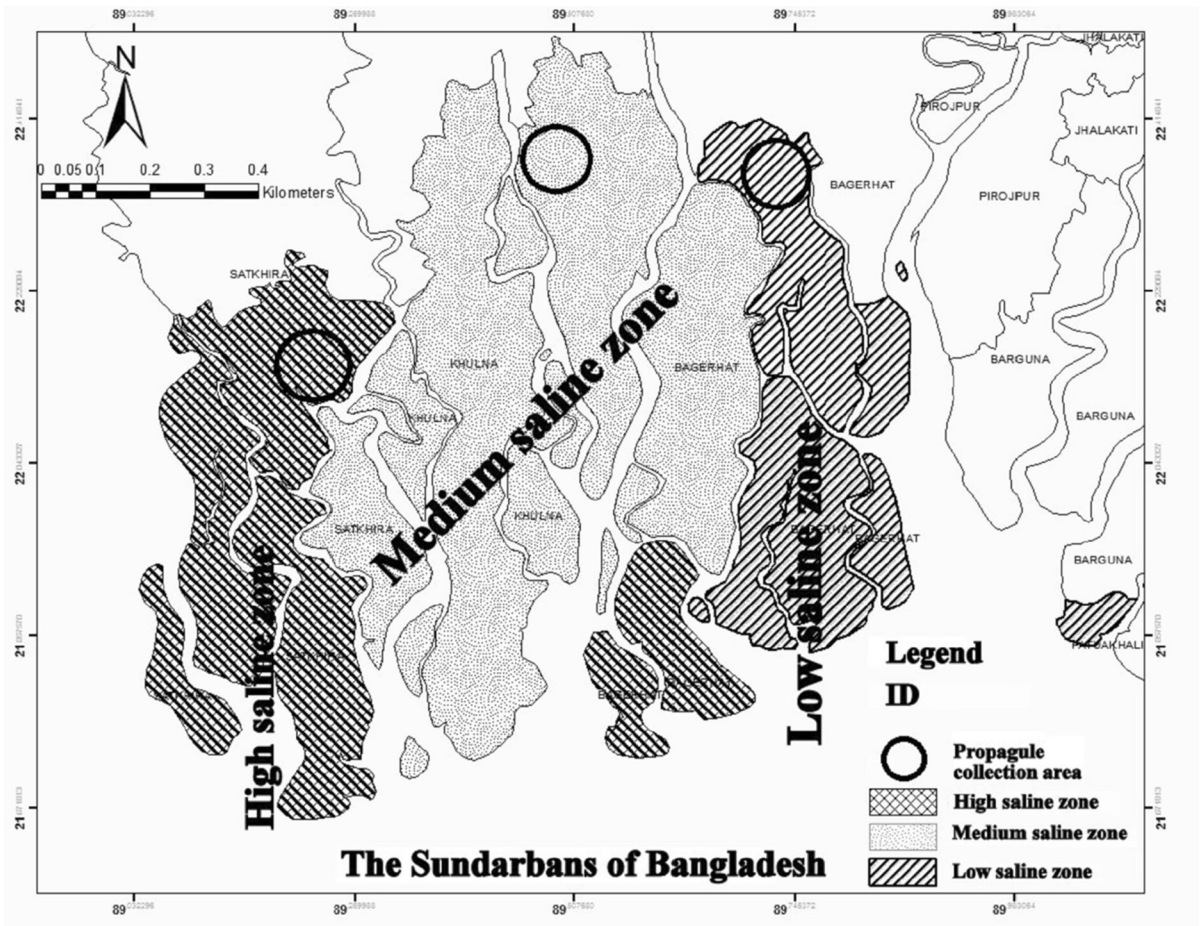


**Fig. 1** The Sundarbans mangrove forest of Bangladesh

high saline zone (HSZ) in the western part (Fig. 1) having salinity from 0.5 to 5, 5 to 18, and 18 to 30 ppt, respectively (Siddiqi, 2001). In this forest, *Heritiera fomes* Buch.-Ham., *Excoecaria agallocha* L., and *Ceriops decandra* (Griff) Ding Hou are the dominant species in LSZ, MSZ, and HSZ, respectively (ODA, 1985; Siddiqi, 2001).

Despite such distinct impact of salinity on mangrove distribution and zonation, *A. officinalis* L. scatters widely as an exclusive pioneer mangrove tree species (Mahmood, 2015) and forms dominant canopies in the LSZ, MSZ, and HSZ of Sundarbans at all salinities (ODA, 1985; Siddiqi, 2001). MacMillan (1974) reported that *A. officinalis* is able to tolerate fluctuating and hyper saline conditions. Therefore, ecological amplitude of this species is very high. Since *A. officinalis* grows as a pioneer species on newly accreted sediments, it creates favorable ecological conditions for the next seral species in mangrove succession, thereby contributing toward sustainable vegetation in the Sundarbans (Siddiqi, 2001; Alam et al., 2017). This forest now supports 234 species of flora, 355 species of birds, 300 species of fish, 49 species of mammals, 87 species of reptiles, 14 species of amphibians, and numerous microorganisms (Siddiqi, 2001).

Beyond the natural habitats in the Sundarbans, *A. officinalis* is the most planted mangrove tree species in the high saline areas of the coastal regions in the ongoing coastal afforestation programs of Bangladesh (Das & Siddiqi, 1985). This species is widely distributed in the Indo- pacific regions (Spalding et al., 1997). *A. officinalis* generally grows on new deposits of sediment, thereby stabilizing the coastlines (Thampanya et al., 2006; Das et al., 2014; Alam et al., 2017). Despite having typical ecological significance and adaptability of *A. officinalis* in a wider range of salinity, the variations in morphological and physiological characteristics within this species are still unknown. However, this knowledge would be of particular importance for identifying and selecting more salt-adapted phenotype(s) of *A. officinalis* for coastal afforestation programs in Bangladesh. Salinity in the coastal regions of the country is increasing due to decreasing fresh water flow from the upstreams (Islam & Wahab, 2005; Gopal & Chauhan, 2006; Basar, 2012) which poses a threat to the vegetation of the Sundarbans (Minar et al., 2013). Moreover, this increasing salinity in the coastal regions may create a challenge to select suitable mangrove species for coastal afforestation. Hence, identifying the most salt-adapted phenotypes of *A. officinalis* is of paramount importance for the sustainable ecosystem management of the Sundarbans and also for successful coastal afforestation in the high saline substrates.

It is important to know the regeneration ecology of mangrove species (Pascual, 2016) because successful regeneration determines the establishment of a wetland mangrove plant community (Wall & Stevens, 2015). Hoque et al. (1999) studied the effect of salinity on the germination of *Sonneratia apetala* Buch.-Ham. Mahmood et al. (2014) studied the influence of salinity on the germination of *Heritiera fomes* Buch.-Ham., *Xylocarpus mekongensis* Pierre, *Xylocarpus granatum* K. D. Koenig, and *Amoora cucullata* Roxb in the Sundarbans of Bangladesh. However, knowledge on the propagule morphology and propagule growth initiation traits of *A. officinalis* is still scarce.

Plants show adaptive plastic responses in terms of morphological and physiological characteristics to cope with a variety of environmental conditions (West-Eberhard, 1989; Sultan, 2000; Callaway et al., 2003). Environmental variability induces adaptive phenotypic plasticity of a plant species (Sultan, 2000; Pigliucci, 2001; Snell-Rood et al., 2010) which may have implications in adaptive biological evolution (Chambel et al., 2005). The species in question grows in a variety of saline environments and bears typical ecological significance. We hypothesize that *A. officinalis* growing in high saline conditions is the most salt-adapted phenotype of this species. If such phenotype is identified, *A. officinalis* would be a potential mangrove tree species for continued coastal afforestation in the high saline coastal regions in the future. Therefore, an attempt was undertaken to explore the adaptive phenotypic plasticity of *A. officinalis* focusing on the influence of salinity and maternal origins on propagule morphology and propagule growth initiation traits across the salinity gradient in the Sundarbans of Bangladesh.

## Materials and methods

### Propagule collection

The dominant patches of *A. officinalis* across the salinity gradient in the Sundarbans were identified by

following the Overseas Development Agency (ODA) vegetation map (ODA, 1985) and the salinity map (Fig. 1) to collect the propagules of this species from three different maternal origins, viz., LSZ, MSZ, and HSZ in the Sundarbans. A minimum of 50 mother trees from each of the three saline zones were selected. The propagules of this species were single units (Zabala, 1990), and were collected from those selected mother trees of *A. officinalis* in LSZ (between N 22°22′ 25.0″ and E 89°44′ 35.7″), MSZ (between N 22°28′ 06.1″ and E 89°30′ 52.2″), and HSZ (between N 22°12′ 18.6″ and E 89°11′ 45.5″) of the Sundarbans (Fig. 1) during August, 2015. The collected propagules were then kept zone-wise separately in the laboratory.

## Propagule morphology and viability tests

A completely randomized design was adopted for this experiment. From the collected propagules, 3 samples of 1000 propagules were taken from each of the three saline zones. Length (mm), width (mm), and weight (g) of each propagule were measured. Then, the viability of each propagule was tested by using 0.1% 2, 3, 5-Triphenyl Tetrazolium Chloride solution at 40°C for 6 h in the laboratory. Only red colored propagules were considered as viable (Copeland & McDonald, 2005).

## Propagule growth initiation experiment

Since the propagules of *A. officinalis* are crypto viviparous where embryo grows but does not rupture the pericarp (Naskar & Mandal, 1999; Saenger, 2002), propagule growth initiation is termed instead of germination for this experiment. The experiment was conducted through use of a randomized block design in a glass house in the forest nursery of Khulna University to study propagule growth initiation time (PGIT) which indicates the time required to initiate growth; mean growth initiation time (MGT) which indicates the day at which maximum growth initiation occurred; growth initiation index (GI) which indicates vigorousness and speedy growth initiation of the propagules; and propagule growth initiation percentage (PGIP) which indicates growth initiation success (%) at the end of the experiment. 24 trays (75 cm × 75 cm × 6 cm of each) filled with a 3 cm thick layer of coarse sand were prepared for each saline zone. Therefore, 72 trays were prepared for LSZ, MSZ, and HSZ. From the zone-wise previous collection, 100 propagules were sown in each of the 24 trays prepared for each of the three saline zones. Distilled water was used for 0 ppt treatment level. The other seven levels of salt solution (5, 10, 15, 20, 25, 30, and 35 ppt) were prepared by using crude sea salt (unrefined sea salt) containing all the chemical constituents of sea water. Then, the eight levels of treatments with three replications for each treatment level were applied to the propagules sown in 24 trays for each of the three saline zones. Salinity in each tray was checked and corrected daily. Mean temperature and relative humidity during the experimental period were recorded as 35°C and 66%, respectively. Initiation of both root and shoot was considered as propagule growth initiation. Number of growth initiated propagules were counted and recorded at 24 h interval for 49 days. The propagule growth initiation traits were calculated as follows:

$$\text{PGIT (day)} = \text{Day of first growth initiation} - \text{Day of propagule sowing} \quad (1)$$

$$\text{MGT(day)} = \frac{\sum n_i d_i}{\sum n_i}, \quad (2)$$

where $n_i$ is the number of growth initiated propagules in $d_i$; $d_i$ is the number of days after sowing (Orchard, 1977)

$$\text{GI}\left(\text{propagulate day}^{-1}\right) = \sum \frac{n}{d}, \quad (3)$$

where $n$ is the number of seedling emerging on day d; $d$ is the day after propagule sowing (Karaguzel et al., 2004). PGIP was calculated according to Ellis and Roberts (1981)

$$\text{PGIP} = \frac{\text{Number of growth initiated propagules at the end of the test}}{\text{Total number of sown propagules}} \times 100. \quad (4)$$

## Statistical analysis

IBM SPSS Statistics 20, SAS 6.12 statistical software, and MS Excel were used for statistical analysis. Variation in propagule length (mm), propagule width

(mm) and propagule weight (g/propagule) of *A. officinalis* among three saline zones were analyzed by one-way ANOVA. Propagule Viability Percentage (PVP) and PGIP were transformed into arcsine. PVP was analyzed by one-way ANOVA. PGIT, MGT, GI and PGIP of *A. officinalis* of three saline zones under different salinity treatments were analyzed by two-way ANOVA and correlation to find out the impact of the increasing salinity on the growth initiation traits and their variations between the saline zones. LSD followed by Bonferroni adjustment (sig.$^{b}$) at the 0.05 significance level were performed as post-ANOVA tests for pairwise comparisons in respect of all the studied parameters between saline zones and salinity*zone (origin) interactions at the respective salinity levels. These analyses were performed to find out the variations in the impact of salinity gradient on the propagule morphology, and propagule growth initiation traits of *A. officinalis* in the three distinct saline zones of the Sundarbans.

## Results

### Propagule morphology and viability of *Avicennia officinalis*

The propagule length varied significantly ($P< 0.002$) among LSZ (41.7 ± 1.7 mm), MSZ (34.0 ± 1.5 mm) and HSZ (27.6 ± 1.1 mm) (Fig. 2). Post-ANOVA results (LSD) with Bonferroni adjustment (Table 1) showed that the differences in propagule length were significant between LSZ and MSZ (sig.$^{b}$ = 0.026) as well as between LSZ and HSZ (sig.$^{b}$ = 0.001), while this difference between MSZ and HSZ was not significant (sig.$^{b}$ = 0.059).The propagule width varied significantly ($P < 0.002$) among LSZ (31.2 ± 1.3 mm), MSZ (25.1 ± 1.2 mm) and HSZ (19.9 ± 1.2 mm) (Fig. 2). However, our post-ANOVA results (Table 1) showed that the differences in propagule width were significant between LSZ and MSZ (sig.$^{b}$ = 0.041) as well as between LSZ and HSZ (sig.$^{b}$ = 0.002), while this difference between MSZ and HSZ was not significant (sig.$^{b}$ = 0.070).The weight of individual propagule varied significantly ($P < 0.006$) among LSZ (7.4 ± 0.1 g), MSZ (5.7 ± 0.3 g) and HSZ (4.8 ± 0.14 g) (Fig. 2). However, our post-ANOVA results (Table 1) showed that the differences in propagule width were significant between LSZ and MSZ (sig.$^{b}$ = 0.027) as well as between LSZ and HSZ (sig.$^{b}$ = 0.003), while this difference between MSZ and HSZ was not significant (sig.$^{b}$ = 0.220).The propagule viability did not vary significantly ($P > 0.406$) among LSZ (95.0 ± 2.9%), MSZ (93.3 ± 1.7%), and HSZ (90.0 ± 2.9%) of the Sundarbans.

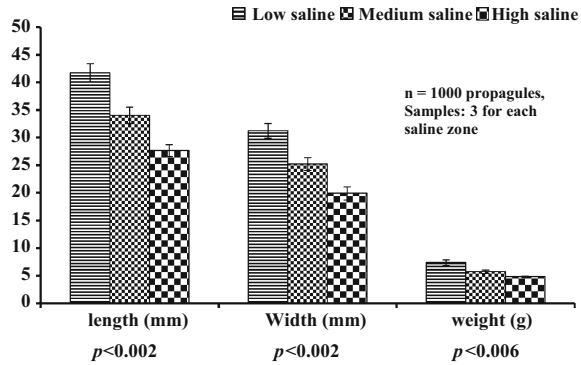


**Fig. 2** Propagule morphology of *A. officinalis* of low, medium, and high saline zones in the Sundarbans: length, width, and weight. Means are significantly different as determined by one-way ANOVA. Vertical bars show standard errors

### Propagule growth initiation traits of *A. officinalis*

Propagule growth initiation time (PGIT) of *A. officinalis* varied significantly ($P < 0.0002$) with the increasing saline treatments, and also among three saline zones (Fig. 3a). After sowing, the propagules of

**Table 1** Pairwise comparisons (LSD) with Bonferroni adjustment (sig.$^{b}$) results between saline zones in respect of propagule length, propagule width, and propagule length

| Between Saline zones | Propagule length (sig.$^{b}$) | Propagule width (sig.$^{b}$) | Propagule weight (sig.$^{b}$) |
|---|---|---|---|
| LSZ and MSZ | 0.026* | 0.041* | 0.027* |
| LSZ and HSZ | 0.001* | 0.002* | 0.003* |
| MSZ and HSZ | 0.059 | 0.070 | 0.220 |

Mean differences are significant (*) at 0.05 level

*A. officinalis* originating from LSZ, MSZ, and HSZ initiated their growth after 6, 5, and 4 days, respectively at 0 ppt level, and 17, 10, and 8 days, respectively at 35 ppt salinity level. PGIT showed positive correlation ($r = 0.670$; Table 2) with the increasing salinity. Our post-ANOVA results (LSD) for salinity*origin interaction with Bonferroni adjustment (Table 3) showed that no significant difference in PGIT values between saline zones was observed from 0 to 10 ppt salinity levels ($sig.^b > 0.05$). However, from 15 to 35 ppt salinity levels, the differences in PGIT between LSZ and MSZ, and between LSZ and HSZ were significant ($sig.^b < 0.05$ at the respective salinity levels), while the difference in PGIT values between MSZ and HSZ was not significant ($sig.^b > 0.05$ at the respective salinity levels) (Table 3). Therefore, the propagules of *A. officinalis* originating from HSZ and MSZ initiated their growth faster at high salinities (lower PGIT values) than those originating from LSZ (higher PGIT values).

**Table 2** Correlation (r) matrices of salinity, PGIP, PGIT, MGT, and GI at $P < 0.05$

| | Salinity | PGIP | PGIT | MGT | GI |
|---|---|---|---|---|---|
| Salinity | 1.000 | | | | |
| PGIP | −0.607 | 1.000 | | | |
| PGIT | 0.670 | − 0.785 | 1.000 | | |
| MGT | 0.736 | −0.779 | 0.958 | 1.000 | |
| GI | −0.729 | 0.685 | −0.909 | −0.970 | 1.000 |

Since PGIT increased with the increasing salinity, it affected MGT correspondingly (strong positive correlation between PGIT and MGT; $r = 0.958$; Table 2). MGT of *A. officinalis* varied significantly

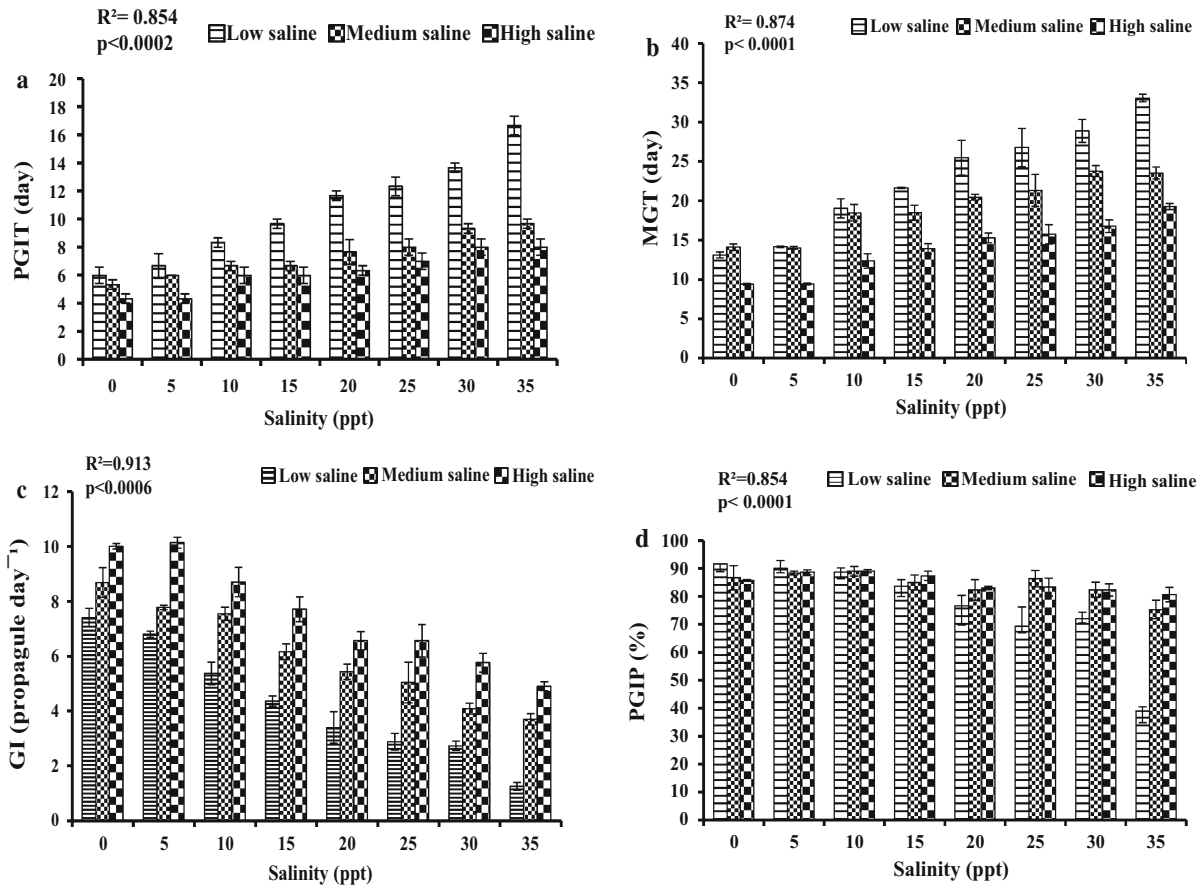


**Fig. 3** Propagule growth initiation traits of *A. officinalis* propagules of low, medium, and high saline zones at different salinity levels **a** PGIT, **b** MGT, **c** GI, **d** PGIP; $n = 100$, replicates = 3 for each treatment level for each of the three saline zones. Means are significantly different by two-way ANOVA. Vertical bars show standard errors

**Table 3** Pairwise comparisons (LSD) with Bonferroni adjustment (sig.[b]) results between saline zones in respect of PGIT, MGT, GI, and PGIP

| Between saline zones at different salinities (ppt) | PGIT (sig.[b]) | MGT(sig.[b]) | GI(sig.[b]) | PGIP(sig.[b]) |
|---|---|---|---|---|
| 0 | | | | |
| LSZ and MSZ | 0.946 | 0.207 | 0.664 | 0.858 |
| LSZ and HSZ | 0.101 | 0.226 | 0.701 | 0.628 |
| MSZ and HSZ | 0.454 | 0.056 | 0.090 | 1.000 |
| 5 | | | | |
| LSZ and MSZ | 1.000 | 1.000 | 1.000 | 0.962 |
| LSZ and HSZ | 0.069 | 1.000 | 1.000 | 1.000 |
| MSZ and HSZ | 0.221 | 0.059 | 0.085 | 1.000 |
| 10 | | | | |
| LSZ and MSZ | 0.946 | 1.000 | 1.000 | 1.000 |
| LSZ and HSZ | 0.213 | 1.000 | 1.000 | 1.000 |
| MSZ and HSZ | 0.946 | 0.109 | 1.000 | 1.000 |
| 15 | | | | |
| LSZ and MSZ | 0.008* | 0.047* | 0.042* | 1.000 |
| LSZ and HSZ | 0.003* | 0.001* | 0.000* | 1.000 |
| MSZ and HSZ | 0.946 | 0.051 | 0.073 | 1.000 |
| 20 | | | | |
| LSZ and MSZ | 0.008* | 0.004* | 0.000* | 1.000 |
| LSZ and HSZ | 0.002* | 0.005* | 0.000* | 1.000 |
| MSZ and HSZ | 0.461 | 0.082 | 0.073 | 1.000 |
| 25 | | | | |
| LSZ and MSZ | 0.007* | 0.007* | 0.020* | 0.016* |
| LSZ and HSZ | 0.002* | 0.022* | 0.012* | 0.038* |
| MSZ and HSZ | 0.868 | 0.275 | 0.167 | 1.000 |
| 30 | | | | |
| LSZ and MSZ | 0.001* | 0.039* | 0.001* | 0.048* |
| LSZ and HSZ | 0.000* | 0.001* | 0.000* | 0.048* |
| MSZ and HSZ | 0.213 | 0.096 | 0.193 | 1.000 |
| 35 | | | | |
| LSZ and MSZ | 0.000* | 0.000* | 0.000* | 0.001* |
| LSZ and HSZ | 0.000* | 0.000* | 0.000* | 0.000* |
| MSZ and HSZ | 0.221 | 0.105 | 1.000 | 0.933 |

Mean differences are significant (*) at 0.05 level

($P < 0.0001$) with the increasing salinity and also among the saline zones (Fig. 3b). Because both PGIT and MGT increased with the increasing salinity, they affected GI (strong negative correlation between PGIT and GI, and between MGT and GI; Table 2). GI of *A. officinalis* varied significantly ($P < 0.0006$) with the increasing salinity and also among the saline zones (Fig. 3c). A strong negative correlation ($r = -0.729$; Table 2) was observed between GI and increasing salinity. Our post-ANOVA results (LSD) with Bonferroni adjustment (Table 3) showed that no significant difference in MGT between saline zones was observed from 0-10 ppt salinity levels (sig.[b] $> 0.05$). However, from 15 to 35 ppt salinity levels, the differences in MGT between LSZ and MSZ, and between LSZ and HSZ were significant (sig.[b] $< 0.05$ at the respective salinity levels), while the difference in MGT between MSZ and HSZ was not significant (sig.[b] $> 0.05$ at the respective salinity levels) (Table 3). The similar result was found for

GI (Table 3). Therefore, the propagules of *A. officinalis* originating from HSZ and MSZ initiated their growth more vigorously at high salinities (higher GI values) than those originating from LSZ.

At the end of the experiment, a significant variation ($p < 0.0001$) in PGIP of *A. officinalis* was observed with the increasing saline treatments and also among the saline zones (Fig. 3d). PGIP was negatively correlated ($r = -0.607$; Table 2) with the increasing salinity. PGIP of the propagules of *A. officinalis* originating from LSZ, MSZ, and HSZ varied from 91.7 ± 2.8% to 39 ± 4.2%, 89 ± 1.7% to 75.3 ± 3.3%, and from 89 ± 0.6% to 80.7 ± 2.6%, respectively across the salinity gradient (from 0 to 35 ppt). Our post-ANOVA results (LSD)for salinity*origin interaction with Bonferroni adjustment (Table 3) showed that no significant difference in PGIP between saline zones was observed from 0 to 20 ppt salinity levels irrespective of propagule origin ($sig.^b > 0.05$). However, from 25 to 35 ppt salinity levels, the differences in PGIP between LSZ and MSZ, and between LSZ and HSZ were significant ($sig.^b < 0.05$ at the respective salinity levels), while the difference in PGIP between MSZ and HSZ was not significant ($sig.^b > 0.05$ at the respective salinity levels) (Table 3).The highest growth initiation (%) of the propagules of *A. officinalis* of LSZ (91.7 ± 2.8%) was recorded at 0 ppt salinity level, while those of MSZ (89 ± 1.7%) and HSZ (89 ± 0.6%) were recorded at 10 ppt salinity level. The growth initiation success (%) of the propagules originating from HSZ and MSZ was higher at high salinities than those from LSZ. For example, PGIP of the propagules originating from HSZ and MSZ were 80.7 and 75.3%, respectively at 35 ppt salinity, while that from LSZ was only 39% at the same salinity treatment level.

## Discussion

Propagule size and weight were different for *A. officinalis* among the three different maternal origins (LSZ, MSZ, and HSZ) of propagule material across the distinct salinity gradient in the Sundarbans. The length, width, and weight of the propagules of *A. officinalis* varied significantly between the saline zones. The LSZ had significantly larger and heavier propagules, while the MSZ and HSZ had the smaller and lighter propagules. Shin & Kim (2013) found variations in seed size and weight of *Cicuta virosa* L. from three different habitats. Mangrove plants grow in saline water conditions where they have to invest a lot of metabolic energy cost for desalination and uptake of water against an osmotic gradient (Saenger, 2002). So, mangroves disproportionately allocate photosynthates in their different parts as an adaptation to cope with different degrees of stressful saline environments (Siddiqi, 2001). These stressful conditions regulate plant morphology (Tomlinson, 1986), seed weight and size (Alonso-Blanco et al., 1999). The salinity stress in LSZ is low compared to that in MSZ and HSZ in the Sundarbans. So, *A. officinalis* growing in the LSZ has to expend comparatively low amount of metabolic cost for desalination and water uptake. Hence, this species in the LSZ can easily deposit more photosynthetic product in its different parts. The larger and heavier propagules of this species in LSZ are the clear evidence of low salinity stress in LSZ in the Sundarbans. However, compared with LSZ, this species growing in the MSZ and HSZ has to invest high amount of metabolic cost for the same purpose because of high salinity stress and consequently has to adjust metabolic energy investment for desalination by reducing deposit of photosynthetic product in its different parts. The smaller and lighter propagules in these zones are the reflection of such adjustment. Therefore, in our study, we found a significant impact of maternal saline environments on the size and weight of propagules of *A. officinalis*. The differences in propagule size and weight of *A. officinalis* suggest that this species shows phenotypically plastic responses to adapt to the salinity gradient in the Sundarbans.

Significant impact of salinity on the propagules growth initiation traits of *A. officinalis* was observed. We found that the increasing salinity remarkably delayed the propagules growth initiation (higher PGIT values with the increasing salinity) (Fig. 3a). Waisel (1972) and Kim et al. (2013) reported that high salt concentration in the medium induces high osmotic potential, ion toxicity and restricts water availability to propagules which, in turn, affect imbibition, enzyme activity and cell division, thereby inhibiting and delaying growth initiation. This delaying effect on propagules growth initiation of *A. officinalis* was not significantly different among the saline zones up to 10 ppt salinity levels (Table 3). So, the propagules initiated their growth almost equally within 10 ppt

salinity levels irrespective of their maternal origins. However, from 15 ppt upward, growth initiation of propagules originating from HSZ and MSZ was significantly faster and more vigorous (lower PGIT and MGT values; higher GI values) than those originating from LSZ (higher PGIT and MGT values; lower GI values) (Fig. 3a, b, c) (Table 3). Quick growth initiation of the propagules of this species is extremely important because Siddiqi (2001) reported that the propagules of *A. officinalis* lose their viability rapidly. Moreover, Tomlinson (1986) stated that *A. officinalis* usually grows on low lying coastal areas which is frequently inundated by tidal water. For a mangrove species to be colonized in such areas, quick growth initiation of propagules and their early establishment are also equally important because propagules are often prone to be washed away by tidal current and to be buried under mud where the rate of sedimentation is high. Therefore, the propagules of *A. officinalis* originating from HSZ and MSZ zones are more likely to colonize in the unstable mangrove ecosystems even under high saline conditions.

We found that PGIP of *A. officinalis* decreased significantly with the increasing salinity treatments and also varied significantly among different saline zones (maternal origins). Bytnerowicz & Carruthers (2014) and Freitas & Costa (2014) observed that the germination success of mangroves decreased with the increasing salinity. Hoque et al. (1999) found decreased germination of *S. apetala* with the increasing salinity. Mahmood et al. (2014) also found decreased germination of *H. fomes*, *X. mekongensis*, *X. granatum* and *A. cucullata* at high salinities. However, in our experiment, the results of post-ANOVA for pairwise comparisons between saline zones at respective salinity level showed that effect of salinity up to 20 ppt on PGIP was insignificant irrespective of propagules maternal origins. The highest PGIP of propagules of *A. officinalis* originating from LSZ was observed at 0 ppt treatment level. This indicates that *A. officinalis* has facultative halophytic characteristics at the life stage in this experiment. However, the highest PGIP of propagules of this species originating from MSZ and HSZ zones were recorded at 10 ppt salinity treatment level. This might happen for the propagules of *A. officinalis* due to their maternal exposure to high salt conditions in MSZ and HSZ of the Sundarbans. Waisel (1972) reported that such variations in propagules growth initiation success within the species are possible when propagules are collected from different saline conditions. He also reported that propagules originating in a saline environment would grow better in that environment.

Propagules growth initiation potential of *A. officinalis* was found to be restrictive to salinity (Fig. 3d). This restrictive salinity regime is a paradox for *A. officinalis* of different origins. For example, PGIP of propagules originating from LSZ was only 39% at 35 ppt salinity treatment level, while the PGIP of propagules originating from MSZ and HSZ were 75.33 and 80.67%, respectively, at the same treatment level. From 25 ppt upward, PGIP values of propagules originating from MSZ and HSZ were significantly higher than that of LSZ. Janousek & Folger (2013) reported that propagule sources have implications on salt adaptability of mangroves during germination. Why the propagules originating from MSZ and HSZ initiated their growth rapidly and vigorously, thereby achieving higher PGIP at high salinities is an important question.

Mangroves accumulate salt as osmolyte to balance transmembrane osmotic potentials (Shan et al., 2008). Saenger (2002) found that *A. officinalis* accumulates salt in its propagules during maturation. The propagules of mangroves absorb salt from their mother trees during their maturation for osmo-regulation with the saline environments in which they will grow (Zheng et al., 1999). The mother trees of *A. officinalis* growing in MSZ and HSZ are likely to accumulate more salt in their propagules in comparison to those growing in LSZ in the Sundarbans. By accumulating salt, the propagules can create an internal saline condition which is hyperosmotic to the external saline environments in which they have to grow and establish. As a result, they can easily absorb water from the growth media and initiate their growth faster. The propagules of *A. officinalis* originating in MSZ and HSZ perhaps adopted this osmotic adjustment mechanism earlier in their growth initiation stage even though they had to initiate their growth in high saline experimental conditions. These salinity*origin interaction effects suggest that the propagules originating from MSZ and HSZ are able to adapt to high saline conditions from their early growth stage.

Proffitt & Travis (2010) observed differences in survival, growth, and reproduction of *Rhizophora mangle* L. among maternal genotypes and termed these differences as plasticity. They emphasized that

this plasticity is extremely important for the maintenance of *Rhizophora* dominance in a wider range of environmental conditions. Rejmánková (2011) reported that habitat environments determine adaptive phenotypes of a species. Huang et al. (2015) studied phenotypic plasticity of two varieties of *Bidens pilosa* L. var. *radiata* based on its germination performance. We found variability in propagule size and weight between different maternal origins of *A. officinalis*. We also found differences in the influence of salinity stress and maternal origins of the propagules on their growth initiation traits. These differences can be inferred as phenotypic plasticity of *A. officinalis*. Compared with LSZ, the propagules originating from MSZ and HSZ initiated their growth quickly and vigorously with greater growth initiation success (%) even at high salinities. These results support our hypothesis that *A. officinalis* which is growing in high saline conditions is the most salt-adapted phenotype of this species. The ability of the propagules originating from MSZ and HSZ to initiate their growth faster and vigorously in high saline conditions could be a mechanism to colonize themselves in fragile mangrove environments. By doing so, *A. officinalis* continued its habitat-creating role in the high saline environments in the Sundarbans. It is predicted that more salt-adapted phenotype of *A. officinalis* will be able to negotiate high salinity regeneration niches in the Sundarbans, thereby continuing its ecological role even in high saline mangrove habitats. We suggest that the propagules of *A. officinalis* of HSZ and MSZ of the Sundarbans be strategically selected for coastal afforestation on potentially high saline substrates in the coastal regions of Bangladesh in the future.

## Conclusion

The propagules of *A. officinalis* originating from LSZ were significantly larger and heavier than those originating from MSZ and HSZ zones in the Sundarbans. Propagule growth initiation traits of *A. officinalis* in terms of PGIT, MGT, GI, and PGIP varied significantly among different salinity treatments as well as among three different maternal origins. The propagules of this species originating from HSZ and MSZ started their growth initiation more rapidly and spontaneously than those from LSZ. *Avicennia officinalis* of HSZ and MSZ is the most salt-adapted phenotype and that of LSZ is the least salt-adapted phenotype. Therefore, *A. officinalis* showed adaptive phenotypic plasticity which enabled this species to cope with different saline environments in the Sundarbans of Bangladesh. The most salt-adapted phenotype of *A. officinalis* proved to be well adapted to high saline environments during their growth initiation. This salinity-regime-specific knowledge on adaptation of *A. officinalis* during propagule growth initiation will be largely useful for its successful regeneration and conservation as well as for coastal afforestation in the increasing saline environments in the future.

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**Compliance with ethical standards**

**Conflict of interests** The authors do not have any conflict of interest on any issue in this article.

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