



Adaptive responses to salinity: nutrient resorption efficiency of *Sonneratia apetala* (Buch.-Ham.) along the salinity gradient in the Sundarbans of Bangladesh

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Abstract *Sonneratia apetala* (Buch.-Ham.) is a major pioneer tree species of the Sundarbans and is found to grow in the less saline zone (LSZ), moderate saline zone (MSZ) and high saline zone (HSZ) of this mangrove forest. This experiment examined the adaptive behaviour of *S. apetala* grown in different saline zones of the Sundarbans in terms of nutrient resorption/re-translocation efficiency (NRE). Samples of topsoil and green and senescent sun leaves were collected from *S. apetala*-dominated stands located in the three saline zones during the pre-monsoon, monsoon and post-monsoon seasons. Soil available nutrients (N, P and K), sodium (Na) concentrations, and NRE of *S. apetala* leaves from the three saline zones during the different seasons were measured in the laboratory. The average available nutrients (N, P and K); Na concentrations in the soil; and NRE of N, P and K showed significant ($p < 0.05$) differences among the saline zones and seasons. The lowest concentrations of N (25.44 $\mu\text{g/g}$), P (5.44 $\mu\text{g/g}$) and K

(0.036 mg/g) and the highest concentrations of Na (0.50 mg/g) were observed in the HSZ during the pre-monsoon season. The highest NREs of N (63.58%), P (45.86%) and K (61.30%) were found in the HSZ during the pre-monsoon season, while the lowest NREs of N (39%), P (26%) and K (35%) were found in the LSZ during the post-monsoon season. The NRE was positively correlated with the available concentration of Na in the soil. Nutrient resorption is an important nutrient-conserving mechanism for mangroves growing under salt stress. This may be the reason that the NRE was comparatively higher in the HSZ than in the LSZ and MSZ. The findings of this study support the conclusion that *S. apetala* has shown adaptive responses among the populations in the LSZ, MSZ and HSZ of the Sundarbans. This adaptive variation enabled *S. apetala* to survive and grow satisfactorily in a wider range in the Sundarbans.

Keywords Adaptation · Nutrient resorption efficiency · Salinity · *Sonneratia apetala* · Sundarbans

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Introduction

The Sundarbans is the world's largest single tract of mangrove forest (Gopal and Chauhan 2006) and is situated in the south-western part of Bangladesh (Mahmood 2015). This forest protects the coastal

regions of Bangladesh against frequently occurring natural disasters such as tropical storms, tidal surges, soil erosion and salt intrusion (Rahman and Biswas 2011). The Sundarbans is rich in floral diversity (Chaffey and Sandom 1985), and its species composition is controlled by hydrology and the level of salinity (Gopal and Chauhan 2006). Based on salinity, the Sundarbans has been divided into less, moderate and high saline zones (Chaffey et al. 1985).

Salinity gradients from freshwater (0 psu) to seawater (35 psu) are an important physical feature of mangrove habitat (Odum et al. 1982). Salinity determines the reproduction and existence of mangrove species (Waisel 1972) and affects morphological and physiological traits by controlling major metabolic processes (Ball and Pidseley 1995). The changes in the morphological and physiological attributes of mangrove species can be an adaptation for the stresses imposed by salinity (Poljakoff-Mayber and Gale 1975).

Currently, the salinity of river water and soil in the low-lying southwest coastal region of Bangladesh is increasing over time due to the reduction in freshwater flow from upstream (Islam and Wahab 2005; Gopal and Chauhan 2006). This increase in salinity will reduce the abundance of the Sundarbans' key species *Heritiera fomes*, the forest's highest-value timber species (Mahmood et al. 2014) and will increase the abundance of the more salt-tolerant species *Excoecaria agallocha*, *Avicennia officinalis* and *Ceriops decandra* (Minar et al. 2013). *Sonneratia apetala* is a fast-growing (Chen et al. 2003), evergreen pioneer tree species that grows well in the three saline zones in the Sundarbans (Das and Siddiqi 1985; Mahmood 2015). As a pioneer tree species, it modifies sites for the establishment of other biota in the process of succession and can successfully reclaim degraded mangrove forest (Zan et al. 2003). This species has constituted approximately 80% of the coastal afforested areas of Bangladesh since 1965 (Das and Siddiqi 1985).

Mangroves develop different adaptive mechanisms to cope with saline environments to uptake and retain nutrients for their essential physiological processes (Tomlinson 1986). Nutrients are used for plant physiological activities, and some portions are stored in different plant organs or returned to the soil through litterfall, which is then partially absorbed by the roots (Breeman 1995). Nutrient concentration in plant tissue

is the result of the balance between nutrient uptake, plant growth and nutrient resorption. These processes are influenced by plant genetic make-up, soil fertility, and other environmental conditions (Hagen-Thorn et al. 2004). Salinity affects cell nutrition, which also varies with type of cell and in accordance with plant-specific location and function (Waisel 1972).

Mangroves are efficient in retaining and recycling nutrients through resorption/re-translocation of N and P prior to leaf abscission (Alongi et al. 1992). The withdrawal of nutrients from senescing leaves and other plant parts prior to abscission allows a plant to use the same unit of nutrient for their physiological requirements (Vitousek 1982). The resorption of nutrients from leaves is the primary source of plant nutrients (Binkley and Sollins 1995; Piatek and Allen 2000), and it becomes an important process in the nutrient dynamics of a forest ecosystem (Killingbeck 1996; Duchesne et al. 2001). This mechanism can be characterized as the most important adaptive strategy for conserving nutrients (especially N, P and K) for necessary metabolic processes of plants in nutrient-limiting sites such as mangroves (Killingbeck 1996). Nutrients, which are resorbed during senescence, are directly available for plant growth and make a species less dependent on current nutrient uptake (Binkley 1986).

Mineral nutrients, especially nitrogen and phosphorus, are usually considered the major regulating factors of vegetation processes at scales ranging from individual to ecosystem (Grime et al. 1997). The rate of nutrient resorption from senescing leaves may also vary with the availability of nutrients in a certain habitat. However, no single study has identified the adaptive responses in the nutrient resorption of *S. apetala* growing in the three saline zones of the Sundarbans. Hence, this type of study will be helpful for understanding the adaptive mechanism of plants at nutrient-limiting sites such as the Sundarbans, and will help to select populations for upcoming coastal afforestation programmes with changing salinity levels. Therefore, the aim of this study was to determine the adaptive variability of *S. apetala* to salinity in terms of resorption of N, P and K.

Materials and methods

Description of the study site

The study site, the Sundarbans, is located between 21°30' and 22°30'N latitude and between 88°10' and 89°51'E longitude (Ghosh et al. 2002), covering an area of 6017 km² (Hussain and Acharya 1994). The mean annual rainfall is 1500 mm, which is seasonally distributed from May to October. The temperature ranges from 18.50 to 35.20 °C in summer and from 12.20 to 28.80 °C in winter. The soil is silty to sandy clay loam, and bulk density, particle density and porosity vary from 1.18 to 1.27 g/cc, 2.31 to 2.52 g/cc and 46–52%, respectively. The soil pH is approximately 7.8 (Siddiqi 2001). Salinity is the most critical environmental factor in the Sundarbans. Considering the level of salinity, the Sundarbans is divided into a less saline zone (LSZ), a moderate saline zone (MSZ) and a high saline zone (HSZ) ranging from 0.5 to 5, 5–18, and 18–30 psu, respectively (Chaffey et al. 1985; Siddiqi 2001).

Sample collection

Collection of leaf and soil samples

Pure stands of *S. apetala* were identified in the three saline zones of the Sundarbans using a vegetation map and a field visit. Green and senescent sun leaves of *S.*

Available nutrients (N, P and K) and sodium (Na) in soil and nutrients (N, P and K) in green and senescent leaves

Available nutrients (nitrogen-N, phosphorus-P and potassium-K) and sodium-Na were measured for soil samples. The collected soil samples were air-dried for two weeks at room temperature and processed according to Mulvaney (1996). Nutrients (N, P and K) were also measured for green and senescent leaves. Subsamples (100 g of each) of leaves (green, senescent) were collected from the sample trees and dried in an oven at 80 °C for 4 days. Oven dried leaf samples were processed and acid digested following Allen (1974). The concentrations of nitrogen and phosphorus in the sample extracts were measured by using a colorimetric method following Baethgen and Alley (1989) and Timothy et al. (1984), respectively, in a UV–VIS spectrophotometer (HITACHI-2900U). A flame photometer (PFP7, Jenway LTD, England) was used to measure potassium and sodium concentrations in the sample extracts.

Nutrient resorption efficiency (NRE)

The percentage of the nutrient pool resorbed (nutrient re-resorption efficiency (NRE)) prior to leaf fall was calculated using the following equation (Ricardo 1992; Wang et al. 2003).

$$\text{NRE \%} = \frac{\text{Nutrient pool in green leaf} - \text{Nutrient pool in senescent leaf}}{\text{Nutrient pool in green leaf}} \times 100$$

apetala were collected from ten randomly selected mother trees from less (N22°37'13.37" and E89°64'53.3"), moderate (N22°48'40.0" and E89°50'316") and high saline zones (N22°17'19.7" and E89°19'50.8") of the Sundarbans during the post-monsoon (August 2016), pre-monsoon (March 2017) and monsoon season (June 2017). A 5 cm diameter soil core sampler was used to collect the topsoil up to a depth of 20 cm. Soil samples were collected at the same location and time as leaf sample collection.

Statistical analysis

NRE, nutrients (N, P and K), and Na concentration in soil samples from different saline zones and different seasons were compared by two-way Analysis of variance (ANOVA) followed by Duncan's Multiple Range Test (DMRT, $p < 0.05$) using SAS (6.12) statistical software. Correlations among the soil nutrients (N, P and K), sodium and nutrient resorption efficiency were performed using IBM SPSS-20 Statistical software.

Result

Nutrients (N, P and K) in soil

Significant ($p < 0.05$) differences in soil available nitrogen (N), phosphorus (P) and potassium (K) concentrations were observed among the saline zones and seasons. The highest N ($51.60 \mu\text{g/g}$), P ($17.21 \mu\text{g/g}$) and K (0.089 mg/g) concentrations were detected in the LSZ during the post-monsoon season, but the lowest N ($25.44 \mu\text{g/g}$), P ($5.44 \mu\text{g/g}$) and K (0.036 mg/g) concentrations were observed in the HSZ during the pre-monsoon season (Fig. 1a,b,c). The nitrogen concentration in the soil showed no significant ($p > 0.05$) difference between the less and moderate saline zones or between the pre-monsoon and monsoon seasons. Phosphorus concentration showed no significant ($p > 0.05$) difference between moderate and high saline zones. However, the K concentration showed significant ($p < 0.05$)

differences among the saline zones and seasons (Fig. 1a,b,c).

Sodium (Na) in soil

A significant ($p < 0.05$) difference in Na concentration was found among the saline zones and seasons (Fig. 1d). The highest concentration of Na (0.50 mg/g) was measured in the HSZ during the pre-monsoon season, but the lowest concentration (0.09 mg/g) was observed in the LSZ during the monsoon season.

Nitrogen resorption efficiency

A comparatively higher nitrogen resorption efficiency was observed for the pre-monsoon season, but no significant ($p > 0.05$) difference was detected between the pre-monsoon and monsoon seasons. Significantly ($p < 0.05$) the highest (63.58%) resorption efficiency was found for the HSZ during the pre-

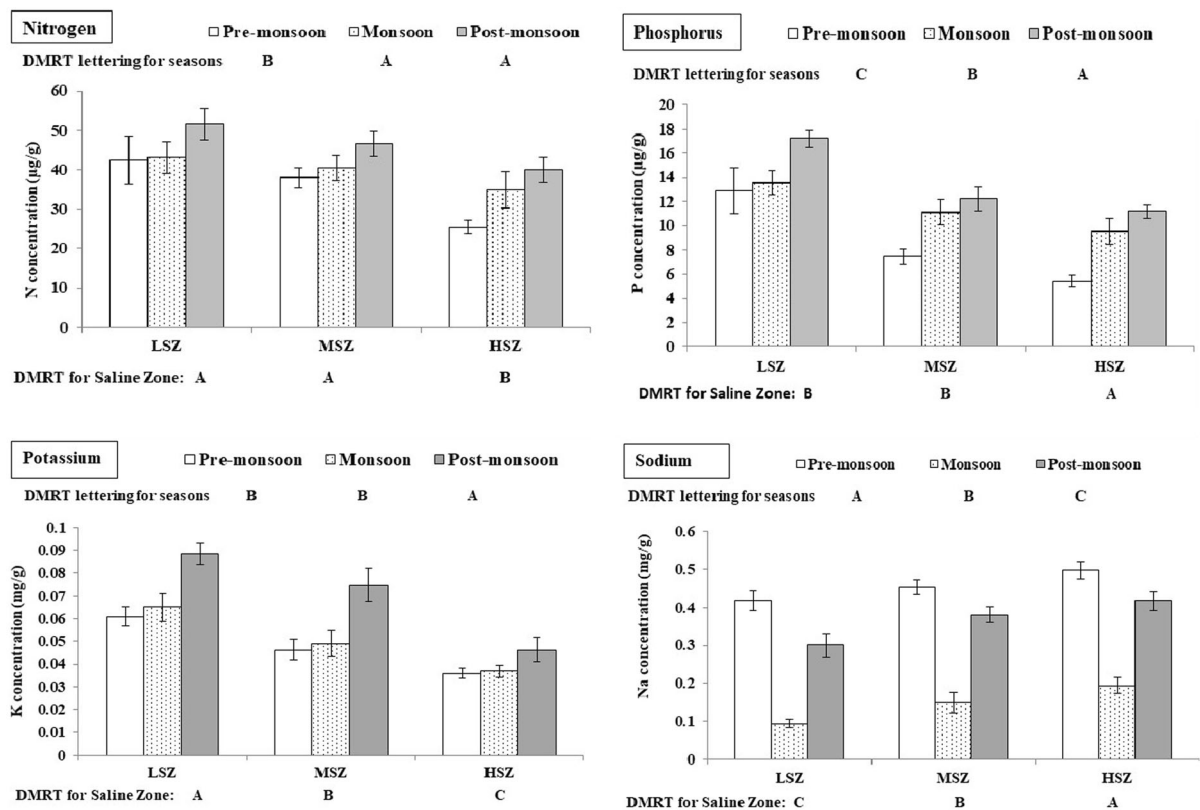


Fig. 1 Mean available concentrations of nitrogen, phosphorus, potassium and sodium in the soil of the less (LSZ), moderate (MSZ) and high saline zones (HSZ) during the pre-monsoon,

monsoon and post-monsoon seasons. Vertical bars represent the standard errors of mean nutrient concentration. Means with the same letter are not significantly ($p > 0.05$) different (DMRT)

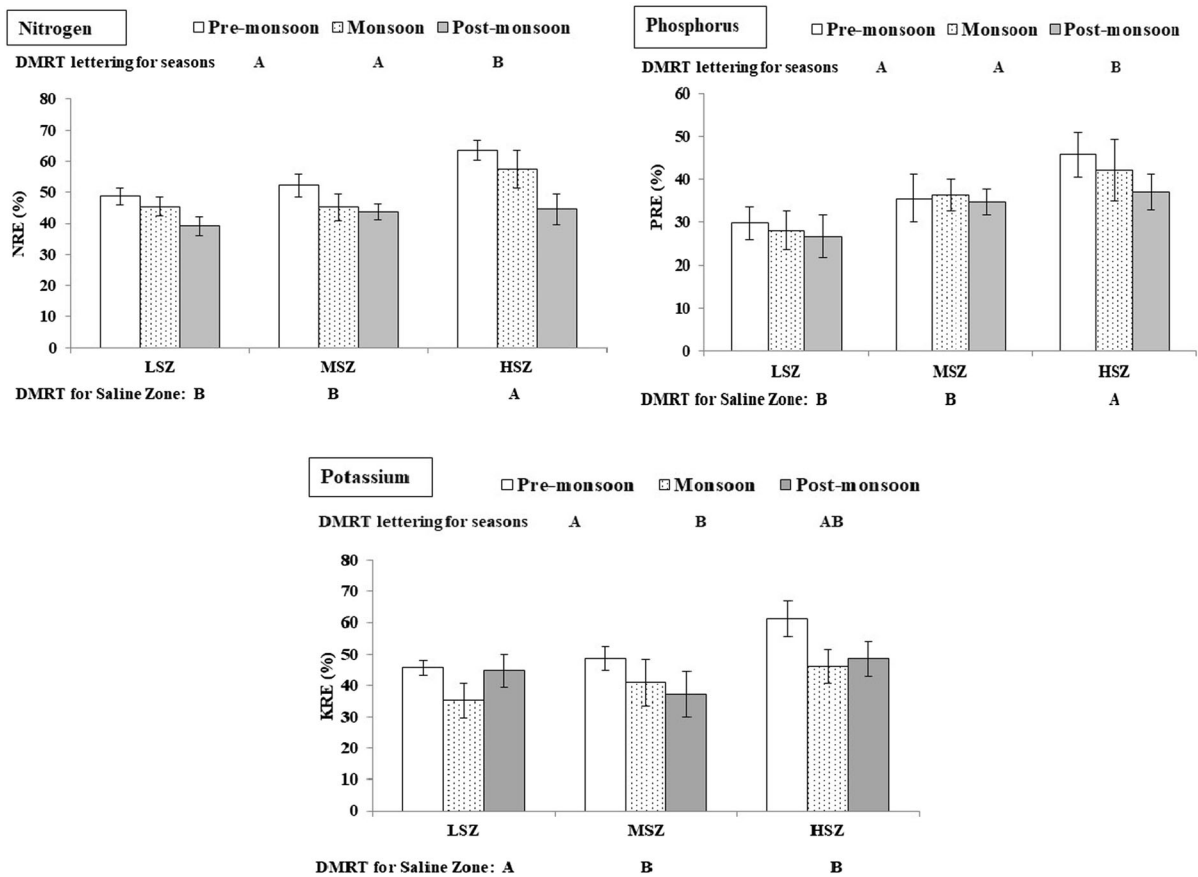


Fig. 2 Mean nutrient resorption efficiency (NRE) for nitrogen, phosphorus and potassium in the less saline zone (LSZ), moderate saline zone (MSZ) and high saline zone (HSZ) during the pre-monsoon, monsoon and post-monsoon seasons. Vertical

bars represent standard errors of mean nutrient resorption efficiency. Means with the same letter are not significantly ($p > 0.05$) different (DMRT)

monsoon season, and the lowest (39.22%) was found in the less saline zone during the post-monsoon season (Fig. 2a).

Phosphorus resorption efficiency

Comparatively, a significantly ($p < 0.05$) higher phosphorus resorption efficiency was observed during the pre-monsoon season. Significantly ($p < 0.05$) the highest (45.86%) resorption efficiency was found for the HSZ during the pre-monsoon season, and the lowest (26.75%) was found in the less saline zone during the post-monsoon season (Fig. 2b).

Potassium resorption efficiency

The potassium resorption efficiency was found to vary significantly ($p < 0.05$) among the salinity zones and seasons. Significantly ($p < 0.05$) the highest (61.30%) resorption efficiency was found for the HSZ during the pre-monsoon season, and the lowest (35.07%) resorption efficiency was found in the less saline zone during the post-monsoon season (Fig. 2c).

Correlations among soil nutrients (N, P and K), sodium and nutrient (N, P and K) resorption efficiency

The N, P and K concentrations in the soil showed significant ($p < 0.05$) negative (-0.87 to -0.91) correlations with the Na concentration in the soil, but the K concentration showed significant ($p < 0.05$)

Table 1 Correlations among the soil nutrients (N, P and K), sodium and nutrient (N, P and K) resorption efficiency

Parameters	Na in Soil	N in Soil	P in soil	K in Soil	NRE for N	NRE for P	NRE for K
Na in soil	1.00						
N in Soil	− 0.87*	1.00					
P in Soil	− 0.91*	0.74	1.00				
K in Soil	− 0.89*	0.79*	0.83*	1.00			
NRE for N	0.79*	− 0.69*	− 0.80*	− 0.71*	1.00		
NRE for P	0.68*	− 0.81*	− 0.84*	− 0.74*	0.70*	1.00	
NRE for K	0.82**	− 0.82*	− 0.77*	− 0.81*	0.65	0.87*	1.00

*Correlation is significant at the 0.05 level (2-tailed)

positive correlations (0.79 to 0.83) with the N and P concentrations in the soil. Significant ($p < 0.05$) positive correlations (0.68 to 0.82) were observed between nutrient (N, P and K) resorption efficiency and Na concentration in soil. Conversely, significant ($p < 0.05$) negative correlations (−0.69 to −0.84) were observed between nutrient (N, P and K) resorption efficiency and N, P and K concentrations in soil (Table 1).

Discussion

Mangrove soil contains a lower concentration of nutrients (Alongi et al. 1992) that varies greatly among and within mangrove forests (Feller et al. 2003; Boto and Wellington 1983; McKee et al. 1993). Mangrove soils are typically saline, anoxic and acidic and are frequently waterlogged. Salinity creates negative osmotic potential that reduces the uptake ability of water and nutrients by mangrove plants (Waisel 1972). Nitrogen (N) and phosphorus (P) are limiting in all mangrove ecosystems (Krauss et al. 2008).

In our study, lower concentrations of available nutrients (N, P and K) in soil were detected in the HSZ compared to the LSZ and MSZ during the pre-monsoon season. The lower concentration of available nitrogen ($25.442 \pm 1.73 \mu\text{g/g}$) in the soil of the HSZ may be due to the high concentration of cations from the seawater that compete with ammonium (primary form of nitrogen-N) for plant uptake (Holmboe and Kristensen 2002). Much lower concentrations ($5.44 \pm 0.52 \mu\text{g/g}$) of available phosphorus in the soil of HSZ during the pre-monsoon season were detected. Higher saline conditions may immobilize

soil phosphorus for plant use. Symbiotic associations between roots and arbuscular mycorrhizal (AM) fungi are widespread in nearly all soils (Treseder and Cross 2006) and are important for the uptake of immobile nutrients, especially for the solubilization of phosphorus (Smith et al. 2003).

AM fungi have been found only in low-saline mangrove soils (Sengupta and Chaudhuri 2002), but the absence of AM fungi in high-saline soil can have a negative influence on the uptake of some nutrients (Bradley et al. 1982). All plants require potassium to maintain intracellular electric neutrality, osmotic regulation, enzyme activation, protein synthesis and photosynthetic metabolism (Leigh and Wyn Jones 1984). In high saline environments, potassium is important for osmotic regulation (Downton 1982) and helps to form the electrical potential that is required to facilitate water uptake against the strong external salt (mostly Na) gradient. Potassium declines in mangroves as well as in other plants due to the loss of chlorophyll and photosynthetic function (Ball et al. 1987). The availability of potassium in mangrove soils is variable, and there is some evidence for potassium limitation in some mangroves (Ukpong 1997).

Mangrove trees are highly productive, and their nutrient-conserving processes are well developed. The resorption of nutrients prior to leaf fall is one of them (Lovell et al. 2010). This is a process in which nutrients resorbed from senescent leaves are directly available for continued plant growth (Hortensteiner and Feller 2002). The nutrient resorption efficiency of *S. apetala* is significantly higher in the HSZ than in the LSZ and MSZ during the pre-monsoon season. Salinity in the Sundarbans varies seasonally and is extremely reduced during the monsoon season in

Bangladesh (Siddiqui 2001). This fluctuation of salinity in the Sundarbans depends on fresh water flow from upstream and the tidal effect (Islam and Wahab 2005; Gopal and Chauhan 2006). The average salinity in the Sundarbans is higher during the pre-monsoon and post-monsoon seasons than during the monsoon season because of the lack of freshwater flow from upstream. Nutrient adsorption to mangrove soil is much lower than that in terrestrial environments due to the high concentration of cations from the seawater that compete for binding sites (Holmboe and Kristensen 2002). As salinity increases, the availability of soil nutrients decreases, and nutrient resorption efficiency in mangroves increases as a nutrient conservation mechanism (Killingbeck 1996). This could be one reason that lower availability of soil nutrients (N, P and K) and higher NRE was observed for all saline zones of the Sundarbans during the pre-monsoon season.

Translocation of nutrients out of senescing leaves back into shoots is an important nutrient conservation mechanism for N and P but is less important for K (Dunbar-Co et al. 2008). Mangroves show lower nutrient resorption efficiency when nutrients become more available in the soil (Feller et al. 1999; Lovelock et al. 2007a). The existence of negative correlations between available nutrients in soil and the respective NRE (Table 1) for those nutrients demonstrate that *S. apetala* has the ability to adopt higher NRE with increasing salinity.

NRE can vary greatly between species, but on average, plants resorb ~ 50% of the nutrients (N and P) from their senescent tissue (Aerts and Chapin 2000). The present study showed the highest percentages of resorption efficiency for nitrogen and phosphorus in the HSZ, which were approximately 60% and 46%, respectively. Rao et al. (1994) compared eight mangrove species with resorption efficiency values of approximately 65%. On the other hand, the nitrogen resorption efficiency of *Avicennia marina* in Kenyan mangroves (Ochieng and Erftemeijer 2002), *Rhizophora stylosa* in Western Australia (Alongi et al. 2005) and *Kandelia candel* in China (Wang et al. 2003) were approximately 69%. The lowest levels of nitrogen resorption efficiency were recorded for *A. germinans* at Twin Cays (approximately 5%; (Feller et al. 2007) and for *A. marina* in New Zealand (20%; Lovelock et al. 2007b). Higher N and P resorption efficiency values indicate that the internal cycling of N

and P can supply a significant fraction of the required nutrients for plant growth in mangroves.

Sonneratia apetala from the three saline zones showed significant variation in nutrient conservation strategy in terms of nutrient resorption efficiency. This may arise from the variation in salt tolerance of the species growing under different levels of salt stress. Johnson et al. (2003) demonstrated that species exposed to stressful environmental conditions express more tolerance of both physiological and morphological conditions than species grown in a favourable environment or non-stress environment. Variations in geographical conditions lead to the evolution of different adaptations to the local environment (Savolainen et al. 2007). Furthermore, local adaptation helps plants to successfully cope with heterogeneous environments across their distribution (Liu et al. 2015). Therefore, *S. apetala* of the HSZ is more adaptable to salinity than those grown in the LSZ and MSZ.

Conclusion

The nutrient resorption efficiency of *S. apetala* has appeared to be an adaptive capacity to the saline conditions of the Sundarbans. Based on the results of this study, it can be concluded that the physiological and morphological traits of *S. apetala* are correlated with the environmental gradient (salinity level), and it is suggested that the adaptation variability of *S. apetala* requires more intensive study at the genetic level.

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