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Research article

Spatio-temporal variation in leaf traits of Sal (*Shorea robusta* Gaertn.) populations in Bangladesh

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Abstract: Plant traits are often studied to understand the mechanisms of adaptation to their environment. The present study examined whether leaf traits (*e.g.* specific leaf area, leaf size, leaf breadth, leaf length, chlorophyll content, water content, relative water content, dry matter content and stomatal size, density, open-close behavior and pore index) of Sal (*Shorea robusta*) differed between Singra and Madhupur Sal forests those were situated in two different geographical locations in Bangladesh. Fully expanded leaves were collected from five different locations within each forest type during May and December. Soil samples were collected at 0–10 cm depth and analyzed for moisture, pH, conductivity, organic carbon, nitrogen, phosphorus, sodium and potassium. Two-way ANOVA showed that forest type had significant effects on leaf breadth, leaf area, specific leaf area, relative water content and dry matter content where all these parameters showed higher values in Madhupur Sal forest excepting dry matter content which was higher in Singra forest. Season also showed significant effects on open-close behavior of stomata with the highest mean value of open stomata in December in both forests. Principal Component Analysis (PCA) done by using the correlations among the leaf traits showed that both Madhupur and Singra forests were separated from each other during may due to leaf morphological variation and both Madhupur and Singra forests showed a similar trend of seasonal variation due to stomatal behavior. Results obtained in the present study suggested that geographical and seasonal variation of leaf traits of *S. robusta* might be related to the climatic factors as well as phenological events and such morpho-anatomical variation in leaf traits could be related to their adaptation.

Keywords: Climate - Deciduous forests - Leaf traits - Madhupur - Seasons - Singra.

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INTRODUCTION

Leaf phenology is important for tropical trees because it reflects the influence of environment on plant functioning and long-term adaptation (Sterck *et al.* 2011, Devi *et al.* 2019). Morphological and anatomical traits of leaf are important phenology that can explain the adaptation of the trees with the environment (Wang 2011). Water is an important environmental factor that influences the adaptation of plants (Wright *et al.* 2001, Ordonez *et al.* 2009). Plants have selected leaf properties in response to water-limiting conditions to reduce water loss (Westoby *et al.* 2002, Wright *et al.* 2002, Sterck *et al.* 2011) or to improve water-use efficiency (Wright *et al.* 2001). Deciduous species show sensitivity to drier climatic condition and show drought avoidance which helps them to drop their leaves when soil water potentials decline during dry seasons (Reich & Borchert 1984). By avoiding dry periods, they sustain high photosynthetic rates during wet seasons when conditions are favourable for growth (Cornelissen *et al.* 1996, Givnish 2002, Markesteijn & Poorter 2009). On the other hand, some data showed that under favorable (wet) conditions *Shorea robusta* Gaertn. behaved like the evergreen plants such as sustaining leaves for longer periods compared to that of the deciduous plants (Singh & Kushwaha 2005, Bajpai *et al.* 2012). Therefore, differences in climatic conditions should be reflected in the leaf traits at geographical

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scales although such information is not substantially available in spite of its relevance for the conservation and management of the tropical forests.

Sal (*Shorea robusta*) is the dominant tree species of the deciduous forests, also known as Sal forests, in Bangladesh. This kind of forest covers an area of about 1,20,000 ha distributed sporadically in different geographical regions of the country (Alam *et al*. 2008). Among them, Singra and Madhupur forests represent two populations of Sal under two distinct climatic conditions, Singra forest is in the district of Dinajpur situated in the northwestern regions under the Barind area while Madhupur forest is in the district of Tangail in the central plain land with the moist climate of the country. We, therefore, tested the hypothesis that due to climatic variation between these two geographic locations, the Sal plants of these two populations would show a difference in leaf physiological, morphological and anatomical traits which could be related with their adaptation. The objectives of the study, therefore, were to (1) compare the leaf physiological, morphological and anatomical traits between Singra and Madhupur Sal forests at two different seasons and (2) investigate the relationships between leaf traits and soil properties of the study area.

MATERIALS AND METHODS

Study site description and collection of leaf and soil samples

Two populations of Sal forests Madhupur and Singra, situated in the districts of Tangail (24° 20' 18.60" N 89° 59' 12.12" E) and Dinajpur (25° 37' 0.12" N 88° 45' 0.00" E), respectively of Bangladesh were selected for the collection of plant and soil samples (Fig. 1). Being about 250 km away from each other, Madhupur Sal forest is situated in the central plain land while the Singra forest was in the Barind area in the north-western part of the country. Both plant leaf and soil samples were collected in two different seasons: pre-monsoon (May) and winter (December) during the year 2016. Average temperature, precipitation and humidity in Madhupur in May were 30ºC, 178 mm and 73%, respectively and those in December were 21ºC, 1.9 mm and 71%, respectively, while in Singra forest those in May were 29ºC, 140.6 mm and 75% and in December were 20ºC, 1.6 mm and 78%, respectively.

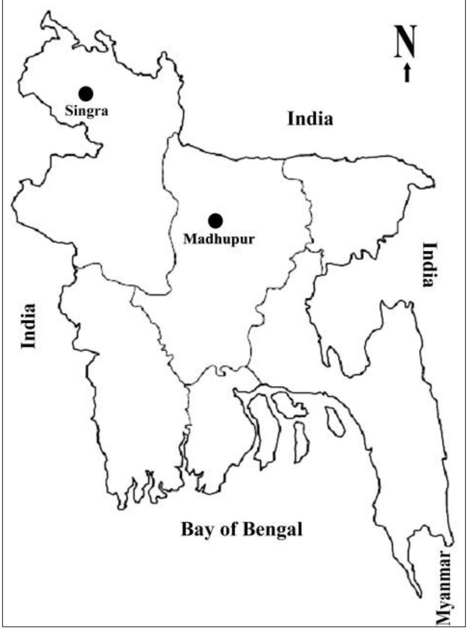

Figure 1. Map of Bangladesh showing the distribution of Sal (*Shorea robusta* Gaertn.) forests selected for the present study.

Plant and soil samples were collected from plots of 10 m × 10 m in size. Each five plots were selected from each of the forest type to collect plant and soil samples in two different seasons. Fully expanded leaves of *S. robusta* were collected from plant and kept in a polythene bag. Composite soil samples were collected at 0–10 cm in depth from the centre of the plot. Immediately after collection from the field, samples were brought to the Ecology and Environment Laboratory at the Department of Botany, University of Dhaka.

Analysis of leaf traits

For the analysis of leaf traits, 5 fresh leaves were selected randomly from the samples collected from each plot. Then, all leaf physiological, morphological and anatomical measurements were done for all these five leaves and then the average value of each parameter was obtained for each plot. For the measurement of leaf length and breadth, each leaf was spread over a plain glass sheet and then a millimeter-scaled ruler was placed along the mid-rib of the leaf to determine the leaf length and breadth was determined by placing the ruler at perpendicular to the position of the mid-rib at the widest point of the leaf. Dry leaf weight was measured after drying the leaf in oven at 80ºC for 24 hours. Leaf chlorophyll content was determined by using a chlorophyll meter (SPAD-502Plus, Minolta, Japan). Leaf size (cm^2) was determined as the mean area of the sampled fresh leaves. Specific leaf area (cm^2 g^{-1}) was calculated as leaf area of the sampled leaves divided by the dry weight of the leaf. Leaf dry matter content (g g^{-1}) was calculated as leaf dry mass divided by leaf fresh mass; leaf water content per unit area (g cm^{-2}) as leaf fresh mass minus dry mass, divided by leaf area. Relative water content was determined as fresh weight minus the dry weight divided by turgid weight minus dry weight. Stomatal length (µm) was measured using five randomly selected stomata in each leaf of the total five leaves per plot. For the measurement of stomatal density (stomata mm^{-2}), the number of stomata per unit area (mm^{-2}) was counted from the images at a magnification of 40 by impression technique. Stomatal pore index (SPI) was calculated by following the formula,

$$\text{SPI} = \text{Stomatal density} \times \text{Stomatal pore area}$$

Analysis of soil properties

Soil moisture content (%) was determined from 10 g fresh soil after oven-drying at 80ºC for 24 hours. Soil pH was determined from suspension of soil: water (1:2, w:v) using pH meter (Hanna pH meter (pHeP). Electrical conductivity (µS cm^{-1}) was measured in suspension of soil with distilled water (5:1, v:w) using conductivity meter (Hanna conductivity meter). Total N (%) was determined by following the Kjeldahl method (Black 1965). Determination of total soil P (%) was done following extraction from 1.0 g finely powered soil with HNO_3 and $HClO_4$. After the development of colour, the absorbance was taken using aspectrophotometer at 440 nm wavelength. The digest solution prepared for the determination of P was also used for the determination of Na and K. Absorvance was measured by using a flame photometer. Soil organic C content (%) was determined by following Walkley and Black method (Black 1965).

Statistical analysis

Two-way ANOVA (Analysis of Variance) was performed to examine the effects of forest types (Madhupur and Singra Sal forests), seasons (May and December) and their interactions. Principal Component Analysis (PCA) was done using correlations of the plant leaf traits and soil properties, separately. Analyses were done by using JMP 4.0 software (SAS Institute, Carry, NC, USA).

RESULTS

Two-way ANOVA statistics showed that forest types had significant effects on leaf breadth, leaf area, specific leaf area, relative water content and dry matter content where mean values of all these parameters were significantly higher in Madhupur forest excepting dry matter content that was higher in Singra forest (Table 1). The seasons showed highly significant effects on percentage of open and closed stomata and also on leaf breadth

Table 1. Two-way ANOVA statistics on the effects of forests (Madhupur Sal forest and the Singra Sal forest), seasons (May and December) and their interaction on the leaf traits of Sal (*Shorea robusta* Gaertn.) plants. Shown are mean values with SEM.

Parameter	**Madhupur**		**Singra forest**		**F-ratio**		
	May	**December**	**May**	**December**	**Forest**	**Season**	**F×S**
Fr.Wt. (g)	2.30±0.189	2.30±0.25	1.86±0.23	2.44±0.17	3.065ns	0.078	8.309*
Dr.Wt. (g)	1.01±0.07	0.94±0.94	0.86±0.11	1.00±0.07	0.165ns	0.252ns	2.402ns
Tu.Wt. (g)	2.80±0.17	2.67±0.24	2.24±0.28	2.930±0.23	0.767ns	0.798ns	6.002*
Chl.	34.50±2.46	34.43±2.32	38.80±2.44	38.82±0.77	2.4ns	0.065ns	0.033ns
Lt. (cm)	18.29±0.67	17.18±1.08	15.66±0.60	18.39±0.43	0.405ns	1.795ns	6.195*
Bt. (cm)	10.65±0.18	11.07±0.35	9.27±0.34	10.48±0.21	11.874***	7.672*	2.477ns
LA (cm^2)	162.55±7.52	160.80±8.83	120.36±9.58	142.84±7.23	9.075***	1.86ns	2.024ns
SLA (cm^2 g^{-1})	32.77±1.93	38.76±2.66	28.73±1.64	28.72±0.85	12.291***	2.911ns	3.835ns
LWC (mg cm^{-2})	2.21±0.08	1.67±0.20	1.65±0.14	2.01±0.06	0.841ns	0.657ns	15.374***
RWC (mg cm^{-2})	180.78±2.93	154.66±13.10	144.85±7.47	150.22±5.44	7.223*	2.0ns	3.896ns
LDMC (mg mg^{-1})	71.81±1.19	83.56±7.63	92.69±4.50	82.13±1.94	5.065*	0.008ns	6.923*
OS (%)	31.99±4.71	77.86±1.30	24.59±1.52	74.36±7.24	1.211ns	88.678***	0.13ns
CS (%)	68.01±4.71	22.14±1.30	75.42±1.52	25.64±7.24	1.211 ns	88.678***	0.13ns
GCLt. (µm)	81.27±6.36	69.70±6.47	79.68±2.98	74.50±4.94	0.082ns	2.219ns	0.323ns
SPI	16.58±3.05	15.56±2.72	19.12±0.86	17.47±3.46	0.651ns	0.234ns	0.013ns
SD	26.17±5.15	31.00±1.08	30.24±1.12	31.30±2.71	0.228ns	0.464ns	0.374ns

Note: Fr.Wt.= Fresh weight; Dr.Wt.= Dry weight; Tu.Wt.= Turgid weight; Chl.= Chlorophyll content; Lt.= Length; Bt.= Breadth; LA= Leaf area; SLA= Specific leaf area; LWC= Leaf water content; RWC= Relative water content; LDMC= Leaf dry matter content; OS= Open stomata; CS= Closed stomata; GCLt.= Guard cell length; SPI= Stomatal pore index; SD= Stomatal density.

(Table 1). Fresh weight, turgid weight, leaf length, leaf water content and leaf dry matter content showed significant effects of interactions between forest type and seasons although no clear patterns were found. Season had significant effects on leaf breadth and open-close behavior of leaf stomata where both leaf breadth and percent of open stomata were significantly higher in December compared to those in May.

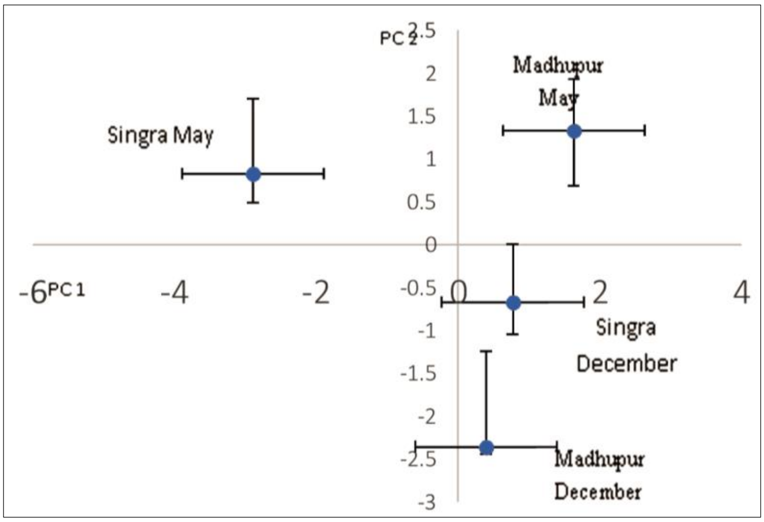

Figure 2. Biplots of Madhupur and Singra Sal forests in the month of May and December obtained from Principal Component Analysis (PCA) done using correlations among the leaf properties of Sal (*Shorea robusta* Gaertn.).

PCA done by using the correlations among leaf properties of *S. robusta* showed that in the month of May, Singra forest was clearly separated from the Madhupur forest along PC1 (Fig. 2). On the other hand, both Madhupur and Singra forests remained together being separated between May and December along PC2.When correlation analysis was done between PCs (1 and 2) and leaf properties (Table 2) it was found that PC1 showed significant correlation with some morphological and physiological parameters such as fresh weight ($r = 0.954$, $P < 0.001$), dry weight ($r = 0.736$, $P < 0.0003$), turgid weight ($r = 0.894$, $P < 0.001$), leaf length ($r = 0.713$, $P < 0.0006$), leaf breadth ($r = 0.908$, $P < 0.001$), leaf water content ($r = 0.730$, $P < 0.0004$) and relative water content ($r = 0.560$, $P < 0.0126$) indicating that the two forest types became different during May due to variation in these leaf properties. On the other hand, PC2 showed significant correlations with open stomata (%) ($r = -0.812$, $P < 0.001$), close stomata (%) ($r = 0.812$, $P < 0.001$), guard cell length ($r = 0.554$, $P < 0.0139$), stomatal density ($r = -0.537$, $P < 0.0178$) specific leaf area ($r = -0.650$, $P < 0.0026$) and leaf water content ($r = 0.509$, $P < 0.0259$) indicating that both the two forest types showed similar seasonal variation due mostly to variation in stomatal movement.

Table 2. Co-efficients of correlations between leaf properties and PC (Principal Component) 1 and PC2.

Parameter	**PC1**	**PC2**
Fresh weight (g)	0.954^{***}	0.253
Dry weight (g)	0.736^{***}	0.221
Turgid weight (g)	0.894^{***}	0.167
Chlorophyll content	-0.009	0.231
Length (cm)	0.713^{***}	-0.106
Breadth (cm)	0.908^{***}	-0.307
Leaf area (cm^2)	0.902^{***}	-0.184
Specific leaf area ($cm^2\ g^{-1}$)	0.214	-0.650^{**}
Leaf water content ($mg\ cm^{-2}$)	0.730^{***}	0.509^{*}
Relative water content ($mg\ cm^{-2}$)	0.560^{*}	0.283
Leaf dry matter content ($mg\ mg^{-1}$)	-0.695^{**}	-0.133
Open stomata (%)	0.256	-0.812^{***}
Close stomata (%)	-0.256	0.812^{***}
Guard cell length (µm)	-0.182	0.554^{*}
Stomatal pore index	-0.172	0.011
Stomatal density	-0.008	-0.537^{*}

Note: *, ** and *** indicate significant, respectively, at 5%, 1% and 0.1% level of probability.

As shown in table 3, among all of the soil properties studied, only pH and phosphorus were significantly affected by both forest types and seasons, organic C only by the seasons and pH was affected by interactions between forest types and seasons. Although pH and phosphorus were affected by seasons and forests types, the larger effects were by seasons. Mean value of soil pH was higher in December (5.04) than May (4.98) in Madhupur forest, however, in Singra forest, it was higher in May (5.42) and lower in December (4.68). Mean value of soil organic C was higher in May in Singra (0.88%) and Madhupur (0.77%) forests and lower in December in Singra (0.67%) and Madhupur (0.59%) forests. Mean value of soil phosphorus was higher in December in both Singra (0.95%) and Madhupur (0.91%) forests and lower in the month of May in Singra (0.89%) and Madhupur (0.60%) forests.

Table 3. Two way ANOVA statistics on the effects of forest and season and their interaction and mean values (±SEM) of the soil properties of the Madhupur and the Singra Sal forests.

Soil parameter	**Madhupur**		**Singra**		**F-ratio**		
	May	**December**	**May**	**December**	**Forest**	**Season**	**F×S**
Moisture (%)	15.89±1.22	9.98±1.35	14.79±0.42	8.72±1.21	0.892ns	23.005ns	0.004ns
pH	4.98±0.09	5.04±0.07	5.42±0.11	4.68±0.14	0.134**	9.482**	13.295**
Conductivity (µS cm^{-1})	29.47±2.39	41.4±23.31	34.28±3.74	20.32±0.72	0.643ns	0.010ns	1.630ns
Organic C (%)	0.77±0.06	0.59±0.11	0.88±0.06	0.67±0.04	2.0ns	7.332**	0.040ns
Available N (%)	0.02±0.01	0.02±0.00	0.03±0.00	0.02±0.01	2.868ns	0.548ns	0.286ns
Phosphorus (%)	0.60± 0.07	0.912±0.09	0.88± .053	0.95± .04	6.208*	9.188**	3.717ns
Sodium (%)	6.60± 1.96	4.292±0.90	3.71±0.31	7.11± 2.07	0.001ns	0.099ns	2.709ns
Potassium (%)	26.73 ±3.48	37.669±2.36	44.72± 1.72	44.52± 2.40	17.657ns	3.306ns	3.553ns

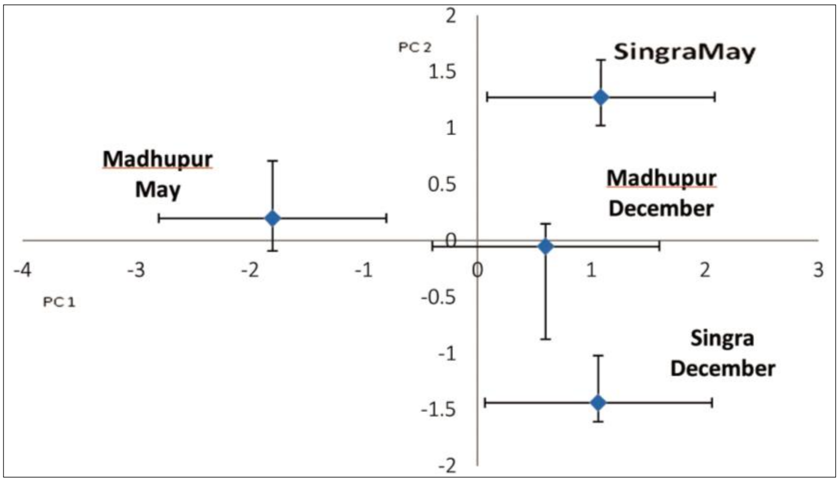

Figure 3. Biplots of Madhupur and Singra forests in the month of May and December obtained from Principal Component Analysis (PCA) done using correlations among the soil properties of the two forests**.**

PCA done by using the correlations among soil physico-chemical properties (Fig. 3) showed that soil of Madhupur in May was clearly separated from that of Singra in both May and December along the PC1. On the other hand, along the PC2, soil of Singra in May was clearly separated from that of the month of December. Coefficients of correlation of soil properties with PC1 and PC2 (Table 4) showed that PC1 had significant correlations with soil moisture ($r = -0.620$, $P < 0.001$), phosphorus ($r = 0.892$, $P < 0.001$), potassium ($r = 0.837$, $P < 0.001$), sodium ($r = -0.184$, $P < 0.001$), available N ($r = 0.525$, $P < 0.008$) and phosphorus ($r = 0.892$, $P < 0.001$). On the other hand, PC2 showed significant correlation with soil pH ($r = 0.684$, $P < 0.001$), conductivity ($r = 0.559$, $P < 0.005$) and organic carbon ($r = 0.745$, $P < 0.001$). Data, thus, indicated that PC1 represented the major nutrient status while PC2 represented the soil chemical conditions of the two forest soils. Madhupur forest showed seasonal variation for nutrient status and Singra forest showed strong seasonality due to changes in chemical conditions like pH and organic C content.

Table 4. Co-efficients of correlations between soil properties and PC (Principal Component) 1 and PC 2.

Soil properties	**PC1**	**PC2**
Moisture (%)	-0.620***	0.330
pH	0.323	0.684***
Electrical conductivity (µS S^{-1})	0.039	0.559**
Organic C (%)	0.073	0.745***
Available N (µg g^{-1})	0.525**	0.045
Phosphorus (%)	0.892***	-0.016
Sodium (%)	-0.184	-0.339
Potassium (%)	0.837***	-0.196

Note: *, ** and *** indicate significant, respectively, at 5%, 1% and 0.1% level of probability.

DISCUSSION

Leaf traits of plants are influenced by environmental factors such as temperature (Li & Bao 2014), light intensity (Lusk *et al.* 2007, Bajpai *et al.* 2012) and water status (Bajpai *et al.* 2012, Bajpai *et al.* 2017). Therefore, leaf traits explain the adaptation mechanisms of plants under resource limitation such as water deficit conditions at spatial scale. Some studies have investigated how morphological traits of the leaf economic spectrum, such as leaf area, and specific leaf area, vary across large geographical scales and ecosystems and adapt to environmental factors (Farquhar *et al.* 2002, Gorsuch *et al.* 2010). Data of the present study showed that the populations of *S. robusta* distributed in different geographical locations differed in leaf morphological traits which could be explained by the difference in climatic conditions between the locations.

The present study revealed that leaf breadth, leaf area, specific leaf area and relative eater content were significantly higher in the Madhupur Sal forests than the Singra Sal forest. Since soil properties, except, pH and P content, most other soil physical and chemical properties including soil moisture content investigated in the present study did not show significant difference between the forest types results, thus, indicated that other factors like climatic condition could have differential impacts on the leaf morphological traits between the two forest types. The Madhupur forest is in the moist climate zone while the Singra forest was in the Barind area which is characterized as dry climate compared to other parts of the country (Rahaman *et al*. 2017). The average monthly rainfall of Singra forest during the months of sampling was lower than that of the Madhupur forest while that of temperature was also higher in Singra forest than that of the Madhupur forest. The functional traits of plant communities are associated with the changes in climatic factors such as light and temperature (Lusk *et al.* 2007, Bajpai *et al.* 2012, Li & Bao 2014). The data that soil moisture content was comparable between the two forest types could be associated with some local factors such as vegetation cover, wind, sunlight and humidity and soil type as well. The higher SLA value of the Sal plants of Madhupur forest indicated that this population was more efficient in water use than that of the Singra forest. It is widely recognized that a large leaf area can enhance solar energy capture (Yang *et al*. 2014), however, it also increases evapotranspiration rate. The higher leaf area of the Sal plants of Madhupur forest indicated that in addition to higher photosynthetic activity, transpiration rate was also higher in this forest. Such higher transpiration rate might have negative impact by reducing soil moisture content in the Madhupur forest soil. Leaf morphological traits including leaf area and specific leaf area reflect the strategies of leaf construction and photosynthesis, respectively (Westoby & Wright 2006, Hernández-Vargas *et al*. 2019). The smaller average leaf area of the Sal plants in the Singra forest might help this plant to reduce transpiration rate since this forest was in arid zone. The higher mean value of leaf dry matter content found in Singra forest indicated greater investment of primary productivity. The significantly higher P content in the soil of Singra forest might have influenced positively the dry matter content of this forest. The greater dry matter content in the leaf of Singra forest compared to that of the Madhupur forest indicated that this plant invested more photoassimilate in leaf and this phenomenon might not be in favor of adaptation of the Sal plants in this region.

Leaf anatomical traits such as stomatal length, stomatal density and stomatal pore area index (SPI) reflect the long-term adaptation of leaf stomatal morphology and photosynthetic capacity (Westoby & Wright 2006, Hernández-Vargas *et al*. 2019). Therefore, it was expected that percentage of open stomata would be lower during December than that in the month of May to reduce transpiration during dry season. However, the present study showed the highest percentage of open stomata during December in both these forest types. This seasonal variation in stomatal open-close behavior might be related with the growing season of the leaf of Sal plants of the two forests. Perhaps leaves were more mature during December compared to that of the month of May when most of the stomata were found mature too. Actually, the month May was in the pre-monsoon season when perhaps leaves were not mature enough for the stomata to be fully functional.

Leaf area and specific leaf area may reflect plant photosynthetic capacity on large geographical scales (Wang 2011). Relatively high leaf area and specific leaf area may enhance plant photosynthetic capacity and primary productivity (Wilson *et al*. 1999). Some studies have demonstrated that specific leaf area is negatively correlated to leaf life span at species level (Reich *et al.* 1997, Shipley *et al.* 2006, Curtis & Ackerly 2008). Therefore, it might be postulated here that greater specific leaf area in the Madhupur forest than Singra forest might cause the lower leaf life span of Sal plants than that of the Singra forest, although further study is needed to confirm such hypothesis.

The highest amount of soil organic carbon found in the month of May in both Madhupur and Singra forest compared to that in the month of December might be due to the accumulation of litter produced from the leaf fall that happened during winter. It was also reported that leaf fall did not completely start in the month of

December since winter season included the months starting from November to February. The higher amount of soil organic carbon in Singra forest than that of Madhupur forest was also consistent since Singra forest was under protected area and hence litter collection by the local people was lower than that in the study area of the Madhupur forest which was not under any management. Similar reason was perhaps responsible for the greater amount of soil P in Singra forests. The greater amount of soil P in the month of December might be related to other factors such as exchangeable and soluble Al, Fe and Ca (Smithson 1999). Although pH value did not vary largely between seasons in Madhupur forest, it showed comparatively greater effects of seasons with the highest in May and lowest in December in Singra forest soil.

CONCLUSION

The results obtained in the present study demonstrated that climatic factors play significant role in influencing leaf traits of *S. robusta* indicating the sensitiveness of the population of the species to the environmental factors. This might be related to the climatic factors as well as phenological events and such morpho-anatomical variation in leaf traits could be related to their adaptation. Results obtained from the present study are thus relevant for the management and conservation of the deciduous forests in the tropical regions.

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