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Germination and growth responses to water stress of three agroforestry tree species from Bangladesh

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A R T I C L E I N F O

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A B S T R A C T

Globally, tree plantations are considered one of the most effective solutions in tackling the climate crisis, and by incorporating trees, agroforestry plays an essential role in mitigating climate change. However, the productivity and sustainability of this commendable solution are often impeded by the wide range of abiotic stresses, including drought. Species selection is always considered as one of the major challenges in a drought-prone area to ensure maximum productivity and halting tree mortality. In this study, seedling responses such as germination, survival, and growth were examined for *Swietenia macrophylla, Acacia nilotica* and *Pithecellobium dulce* in variable soil moisture regimes with 100%, 50% and 25% soil water content (SWC). Despite complete failure of germination at 25% SWC, *S. macrophylla* showed a significantly higher germination percent at both 100% and 50% SWCs ($p < 0.05$). Irrespective of species, the 25% SWC showed reductions of germination percent, survivability and total dry biomass in comparison with the higher moisture regimes. The study also showed that *P. dulce* and *A. nilotica* seedlings were able to survive and maintain growth at low moisture regimes. The significant interaction effect in most parameters highlighted that both species and moisture regimes played an important role in germination and total biomass production, but this interaction had an insignificant effect on the survivability of all species. The result from this study highlights that species-specific responses to water stress could contribute to the species selection policies in drought-prone areas.

1. Introduction

Worldwide atmospheric water demand and terrestrial evapotranspiration have increased in the last few decades, largely through climate warming (Greve et al., 2014, Novick et al., 2016, Trenberth et al., 2014), which may profoundly change the soil water resources available for vegetation growth (Wu et al., 2018). This water-stressed situation has become severe in areas of the world that are susceptible to climate change. Among all countries in the world, Bangladesh is considered to be the sixth most vulnerable to climate change, according to the Global Climate Risk Index (GCRI) (Kreft et al., 2017). In part, this is because there has been a steady increase in temperature, and change in precipitation patterns, during the last few decades throughout Bangladesh (Shahid, 2010, Rahaman et al., 2016). Surface and groundwater depletion have led to severe drought in the north-western region (Hoque et al., 2020, Miah et al., 2017). Moreover, with the existing climate modelling scenarios, the frequency of climate-induced water stress is likely to increase in the next few decades (Shahid, 2010, Rahman and Lateh, 2017), which can reduce agricultural crop production. Based on tree-ring analysis, Islam et al. (2019) found declining radial growth and changes in anatomical features in *Chukrasia tabularis* in the northern tropical forest in Bangladesh. Therefore, along with agricultural crops, perennial trees are subjected to drought, thus hindering the productivity of agroforestry systems and affecting the livelihood of the local people.

Agroforestry is considered as a pathway to regaining forest cover in Bangladesh, which has lost about 40% of forest area in the last century (Reddy et al., 2016). Most of the preferred agroforestry species are exotic in Bangladesh (Leuschner and Khaleque, 1987, Salam et al.,

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2000). This is because, they are considered to provide faster benefit to farmers than that of many native species (Nair, 1993); also, they often ameliorate the ecological environment, e.g. carbon sequestration (Rahman et al., 2015). *Acacia nilotica* L., *Pithecellobium dulce* (Roxb.) Benth., and *Swietenia macrophylla* King. are common tree species planted in woodlots, roadside plantations, homestead and other agroforestry systems in Bangladesh as they provide substantial socio-ecological benefit (Rahman et al., 2015, Hossain et al., 2009, Hossain et al., 2008). *Acacia nilotica* and *P. dulce* are renowned drought-tolerant species commonly planted in the semi-arid and arid zones in the world. They also have been successfully grown on coastal islands and degraded mangrove land in Bangladesh (Islam et al., 2014). On the other hand, *S. macrophylla*, originating from the Amazon, is reported to thrive in a wide range of habitats (Mayhew and Newton, 1998). Soil water is a limiting factor for successful regeneration and establishment to raise successful plantations of these species in Bangladesh. Information about species-specific responses to water stress during the germination and seedling stages is indispensable to screen suitable species for water-limited environments (Kozlowski and Pallardy, 1996, Soriano, 2011, Cervantes et al., 1998). However, the question remains open on identifying suitable species in such water-stressed conditions, especially under climate-induced water-stressed scenarios.

Soil water is the key factor and plays a determining role in seed germination, plant growth and development and global plant community distribution (Gaudillere, 1989, Pallardy, 2010). When soil water stress is severe, the resulting metabolism disturbance and photosynthesis can lead to the death of the plant (Jaleel et al., 2008). Overall, water stress changes the functional and physiological traits of plants, and thereby growth and productivity (Brodribb, 2009, Marron et al., 2002). Therefore, the study of these effects of soil water is important to select tree species for agroforestry systems, especially in the drought-prone areas of Bangladesh.

This study hypothesised that there would be significant differences in germination, survival and growth of *A. nilotica, P. dulce*, and *S. macrophylla* with different water stress levels, and these differences are related to the adaptation of these species to drought conditions. Therefore, this study evaluated the effect of three levels of soil water content (SWC) on seed germination, seedlings survivability and total dry biomass of *A. nilotica, P. dulce*, and *S. macrophylla* tree species in order to reveal the mechanisms underlying the adaptation of these species to water stress.

2. Materials and method

The whole experiment was carried out in a forest nursery glasshouse of Khulna University, Khulna (22° 48′ 03.9" N, 89° 32′ 03.8" E) from April to July. The climate of the area is influenced by tropical monsoon and is mostly characterized by hot summers (March-May), monsoonal rainy season (June–October) and mild winters (November–February) (Alam et al., 2005). Throughout the study period, the indoor mean temperature and relative humidity were 34 °C and 59%, respectively.

2.1. Experimental setup

In this experiment, soil water content (expressed as a percentage of maximum soil water content, SWC) was modified to create water stress conditions. 100% SWC was considered as the optimum water supply, whereas 50% and 25% SWC were considered as water-stressed conditions, respectively. Seeds of *A. nilotica, P. dulce* and *S. macrophylla* were collected from healthy trees from the Khulna University campus, Khulna, Bangladesh. Visibly damaged and inferior seeds were carefully sorted and discarded. To reduce seed moisture variability, seeds were soaked in water for 24 h as a pre-sowing treatment. Seeds of *A. nilotica* and *P. dulce* were not scarified to mimic natural germination.

Table 1
Physical and chemical properties of media.

Soil Properties	*Value, Unit*[*]
pH	7.87
Electrical conductivity (EC)	236 ms/cm
Available Nitrogen (N)	23.6×10^{-3} (±0.003) mg/g
Available Phosphorus (P)	1.2×10^{-4}(±0. 00007) mg/g
Available Potassium (K)	13.99×10^{-2} (±0.003) mg/g
Available Sodium (Na)	18.8×10^{-2} (±0.079) mg/g

[*] Parenthesis indicates the value of the standard deviation

2.2. Media preparation

The potting media was prepared by mixing nursery soil which was sandy loam and organic compost at a ratio of 3:1. No fertilisers were added to the potting media. After drying the soil for 24 h at 105 °C, five pots were filled with dried soil. The amount of dry soil required for each pot was calculated by averaging the weights of five pots containing dry soil samples. The average weight of dry soil was 350 g. The basic physical and chemical properties of the soil were also measured and documented (Table 1).

2.3. Determination of soil water content (SWC)

At the onset of the experiment, a maximum soil water content (100% SWC) was determined by the gravimetric method. Five sample pots containing 350 g of oven-dried soil were completely submerged in water until saturation and then taken out of the water to allow the last drops to drain out. After subsequent weighing, the amount of water required to reach field capacity was determined from the weight difference between dry and wet soil. The mean weight indicates the amount of water required to achieve field capacity for 350g dry soil. A half and one-quarter of the water required for 100% SWC were then calculated for 50% and 25% SWC, respectively.

2.4. Experimental design

The pot experiment for the germination test was arranged in a completely randomized design, with species × soil water content as factors with three replications for each treatment. In this way, three species with three treatments and replications, ended up with total of 27 pots. These pots were used for germination studies and each pot contained 30 seeds. After 6 weeks of the germination study, 15 seedlings with similar height were picked from each germination experiment (except 25% SWC for *S. macrophylla* as no seeds germinated) and were transplanted into separate pots with three replications each of 5 seedlings for growth study. The survivability of the seedlings was monitored every day and the growth experiment were continued for another six weeks.

2.5. Water correction

For each treatment, five pots were kept without a seedling as a control to determine the daily water loss due to evaporation. Control pots were weighed on an electronic balance every alternate day. The daily water loss was corrected by calculating water loss from the difference between the average weight and the initial weight of the control pots of the respective SWC. Therefore, every alternate day, the seedlings were adjusted with the calculated amount of water to compensate for water loss for each treatment.

2.6. Measurement

Seed germination was observed and recorded daily. The germination percentage was calculated from the difference between the number of sprouting seeds and the total seeds in the pot. The percentage of survivability was also calculated from the ratio of live seedlings and the initial number of seedlings. At the end of the growth study, the seedlings were collected and washed gently in running tap water to get rid of soil and the fresh weight was measured instantly using a 4-digit digital balance. Then, the seedling samples were oven-dried at 80°C until they reached a constant weight. In this way, the final total biomass was calculated for the respective SWC treatment and species.

2.7. Statistical analysis

Data normality and homoscedasticity were checked by using Shapiro-Wilk and Levene's tests. In case of non-normality, data were appropriately transformed to meet the assumptions of normality and equal variances, and subsequently back transformed to present graphically. The data for germination including model parameters, growth, and biomass were compared by two-way ANOVA at ($p < 0.05$), followed by a least significant difference (LSD) post hoc test.

The completed seed germination percent versus time (germination time course) of three studied species was fitted with a model-free spline method (Kahm et al., 2010). Each curve describes the germination time course using three parameters: lag phase (γ, days), maximum rate of germination (μ, %/day) and maximum germination percent (A, %). Here germination speed is described by a combination of lag phase and maximum rate of germination, whereas germination success is described by the maximum germination percent. By using a cross-validation method, the model-free spline method smooths the curve and avoids systematic errors derived from four-parametric models such as Logistic, Gompertz, modified Gompertz and Richards.

All statistical and graphical operations were carried out in R (3.6.1 for Windows) environment (R Core Team 2019) by using packages 'car' (Fox and Weisberg, 2019) and 'ggplot2' (Wickham, 2016). The spline germination pattern was fitted by using the package 'grofit' (Kahm et al., 2010) and presented in the graphs with the 'ggformula' package (Kaplan and Pruin 2018).

3. Results

3.1. Seed germination

The germination time courses of the three studied species with three SWCs are presented in Fig. 1. The spline curve fitting indicates that the lag parameter (λ) of *P. dulce* was significantly different to *A. nilotica*, with *P. dulce* germination commencing rapidly under all SWCs. However, lag phases for both species were markedly shorter than for *S. macrophylla*, which took one week to commence germination after sowing at both 50% and 100% SWCs and completely failed to germinate at 25% SWC (ANOVA for lag phase, species; $F_{2,16} = 15.02$, $p < 0.001$) (Figure 1, Table 2). The SWC had no significant effect on the lag phase for all three species, but its interaction effect with species was significant (ANOVA for lag phase, SWC: $F_{2,\,16} = 0.71$, $p = 0.5$ and species × SWC, $F_{3,16} = 4.54$, $p < 0.01$) (Table A.1).

Both species and SWC and their interaction had significant effect on the maximum rate of germination (μ) (ANOVA for maximum germination rate, species: $F_{2,\,16} = 7.81$, $p < 0.01$; SWC: $F_{2,16} = 12.02$, $p < 0.001$ and species × SWC, $F_{3,\,16} = 11.71$, $p < 0.01$) (Table A.2). In particular, *S. macrophylla* showed a distinctly higher maximum germination rate compared with the other two species (Table 2). Thus, although it had a longer lag phase before germination, it germinated more rapidly than the other two species once it had commenced germination.

The two-way ANOVA reveals that species had no significant effect on the maximum germination percent (A), however, higher water stress significantly reduced the maximum germination percent in all species (ANOVA for maximum germination percent, species: $F_{2,16} = 2.91$, $p = 0.08$; SWC: $F_{2,16} = 29.61$, $p < 0.001$ and species × SWC, $F_{3,16} = 20.54$, $p < 0.001$) (Table A.3). *Swietenia macrophylla* and *A. nilotica* showed a consistent downward trend in maximum germination with higher water stress, and *S. macrophylla* completely failed to germinate at 25% SWC. In contrast, *P.dulce* had an anomalously high maximum germination per cent at 25% SWC.

3.2. Seedling survivability

At the end of the experiment, the seedling survivability of the studied species varied significantly among SWCs and species (ANOVA for arcsine transformed seedling survivability, SWC: $F_{2,16} = 4.85$, $p < 0.05$ and species: $F_{2,16} = 3.80$, $p < 0.05$) (Table A.5). However, there was no significant interaction effect of SWC and species on seedling survivability (ANOVA for arcsine transformed seedling survivability, $F_{2,16} = 0.51$, $p = 0.68$). Irrespective of species, seedling survivability at 50% SWC showed over 60% survivability in all cases (Fig. 2). *Pithecellobium dulce* generally showed lower survivability than the other two species (Fig. 2).

3.3. Total dry biomass

The two-way ANOVA showed that both SWC and species were significantly different in terms of total seedling dry biomass (ANOVA for natural logarithmic dry biomass, SWC: $F_{2,72} = 166.70$, $p < 0.001$ and species: $F_{2,72} = 40.14$, $p < 0.001$) (Table A.5). Moreover, there was a significant interaction effect of SWC × species on the total dry matter production of the seedlings (ANOVA for natural logarithmic dry biomass, $F_{3,72} = 6.53$, $p < 0.001$). Despite having non-significant ($p > 0.05$) variation between 100% and 50% SWC, a significant reduction of dry biomass was observed at 25% SWC for all species. *S. macrophylla* seedlings had significantly larger dry biomass than that of the other two species ($p < 0.05$) (Fig. 3).

4. Discussion

The results of this study indicate that the studies three species showed variable responses of germination, survivability and seedling biomass under water-stressed conditions.

Availability of moisture is one of the major requirements for successful seed germination. In general, this study indicated that 25% SWC reduced the rate of germination percentage (%) except for *P. dulce*, which is reported as a xerophytic species in nature (Roy and Roy, 2019). It is possible that the resilience of *P.dulce*'s germination to water stress is an adaptation that allows this species to regenerate even under relatively dry conditions. *Pithecellobium dulce* also showed a very rapid onset of germination, especially in 100% and 50% SWC treatments, suggesting that it uses rapid seedling germination under moist conditions as a strategy to avoid drought stress, with seedlings germinating and establishing during short periods when soil water is adequate. In contrast, while *A. nilotica* had similar maximum germination percentage to *P. dulce*, the onset of germination was not as rapid. This result is consistent with Soriano (2011) who classified *P.dulce* as a fast germinating species, whereas two *Acacia* species were classified as slow.

The complete failure of germination for *S. macrophylla* at 25% SWC could be due to the quick desiccation of the seed (Morris et al., 2000). Although seeds received minimal water at 25% SWC, the available moisture was probably not enough to prevent desiccation. Daws et al. (2006) reported that the desiccation sensitivity of woody plant species varied with seed morphology; for example, *A. nilotica* and *P. dulce* have a thicker and harder seed coat in comparison with *S. macrophylla*.

Given moist conditions, *S. macrophylla* germinated more completely than both *P. dulce* and *A. nilotica*. Morris et al. (2000) reported that germination of *S. macrophylla* close to the rainy season was more successful, which indicates the importance of continuous wet weather for successful germination of this species. *Swietenia macrophylla* seed has been

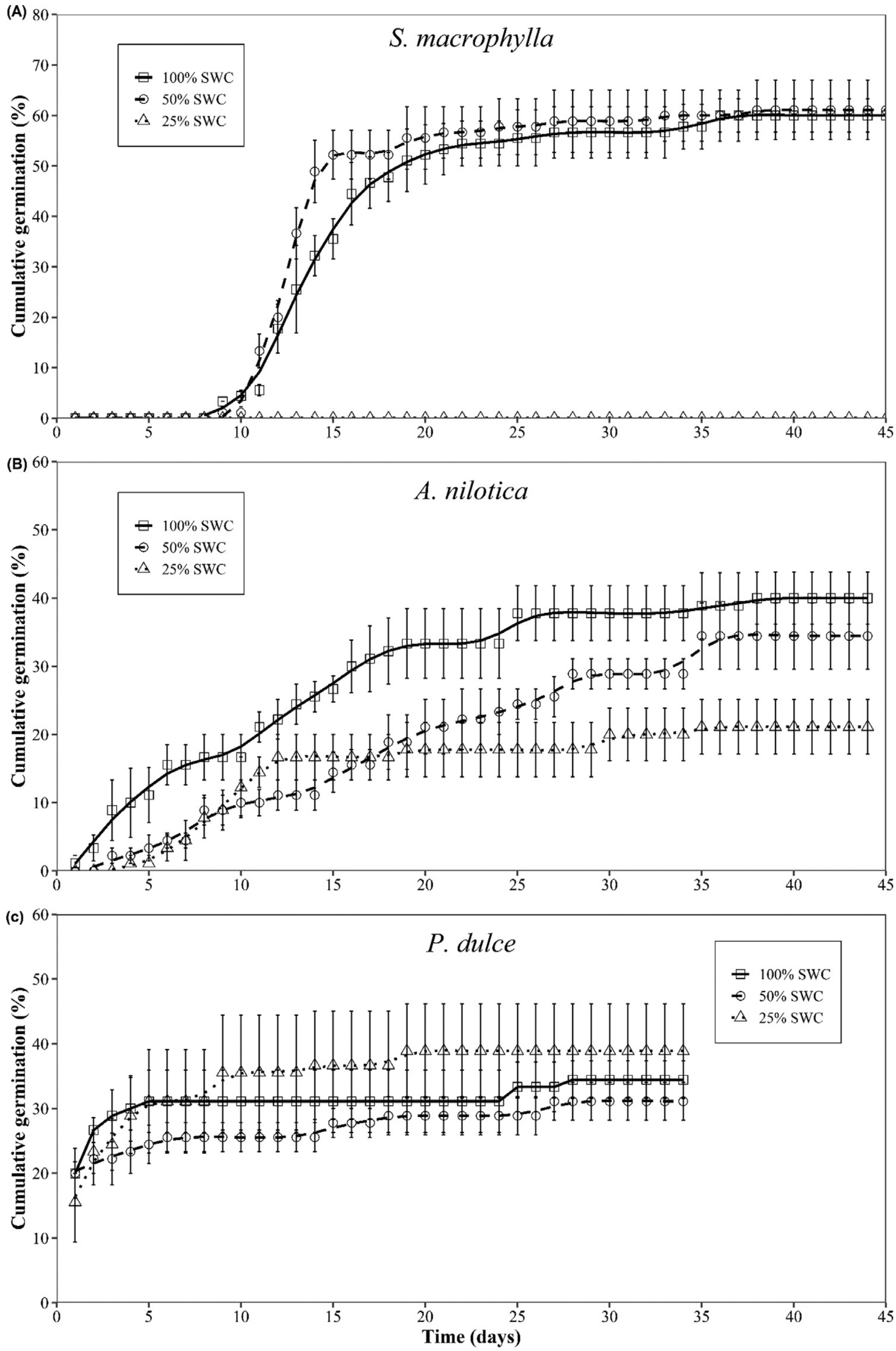

Fig. 1. Cumulative germination percent (mean ± SE) with spline fit of three studied agroforestry species at three levels of SWC for 45 days.

described as recalcitrant (Daws et al., 2005) or intermediate between recalcitrant and orthodox (Marzalina, 2002), where recalcitrant seeds are desiccation sensitive and therefore short-lived, and orthodox seeds are desiccation tolerant and capable of long-term storage in a desiccated condition (Finch-Savage, 2003). This suggests that its germination strategy is to achieve rapid and near-complete germination during moist conditions albeit with a markedly longer lag period compared with the other two species. In contrast, both *P. dulce* and *A. nilotica* have orthodox hard-coated seeds (Soriano, 2011, Ginwal and Gera, 2000) suggesting that even under moist conditions, a proportion of the seed population will not germinate as a bet-hedging strategy.

After germination, the seedlings of *A. nilotica, P. dulce* and *S. macrophylla* responded differently to the applied stressed conditions. Both *P. dulce* and *S. macrophylla* showed increased survivability at 50% SWC than at 100% SWC. This variability may indicate their sensitivity to waterlogged conditions. In nature, many woody tree species are negatively affected by "wet-feet" during their establishment period (Tomar et al., 2003, Godman and Krefting, 1960). Sometimes, the 100% SWC pots seemed to be saturated, due to restricted drainage from the base of the pots. This might have adversely affected seedling survivability.

The survival rate (%) of *P. dulce* dropped sharply from 50% SWC to 25% SWC, therefore 25% SWC was probably critical for *P. dulce*

Table 2
Derived germination parameters for the spline curve fitting of the seed germination data.

Species	% SWC	μ (%/day)	λ (day)	A (%)
S. macrophylla	100	14.87 (±3.05) a	11.04 (±0.28) ab	60.04 (±3.31) a
	50	13.54 (±0.94) a	10.38 (±0.21) ab	61.22 (±5.89) a
	25	-	-	00.00 d
A. nilotica	100	7.52 (±0.49) bc	4.43 (±3.17) bc	40.03 (±3.87) b
	50	2.72 (±0.49) d	7.89 (±5.08) a	34.73 (±4.85) b
	25	3.47 (±0.63) cd	6.13 (±1.40) bc	21.22 (±4.01) c
P. dulce	100	7.77 (±1.90) bc	-2.00 (±0.88) cd	34.44 (±2.94) b
	50	2.20 (±0.48) d	-5.52 (±3.91) d	31.26 (±2.93) bc
	25	8.27 (±2.61) b	3.20 (±2.85) bc	38.98 (±7.24) b

Notes: Fitted parameters for the 3-parameter spline curve for germination where μ signifies the maximum germination rate, λ is the lag phase, and A is the maximum germination (Kahm et al., 2010, Richards, 1959). The similar letters indicate statistically equivalent ($P < 0.05$).

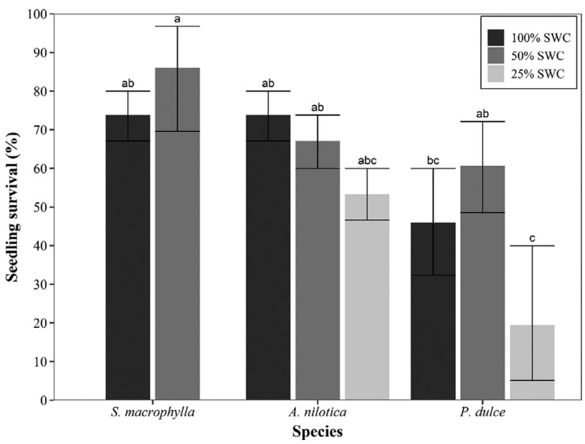

Fig. 2. Percent of seedling survival (mean ± SE) of three agroforestry species at three levels of SWC. *S. macrophylla* had no seedlings at 25% SWC. Different letters indicate significantly different at p <0.05.

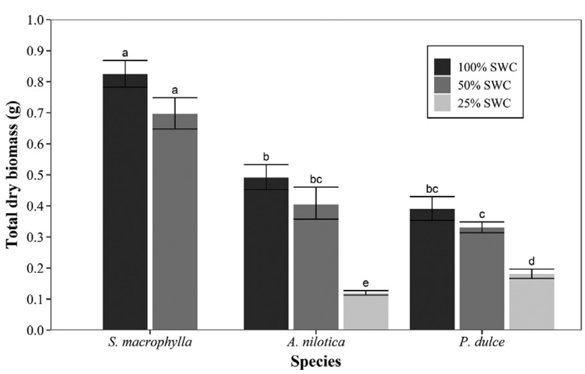

Fig. 3. Total dry biomass (g) (mean ± SE) of three agroforestry species at three levels of SWC.

seedling survival, though *P. dulce* is reported to tolerate aridity (Roy and Roy, 2019). In contrast to *P. dulce, A. nilotica* showed a comparatively minor fall in survival from 50% SWC to 25% SWC, although seedling survivals for these two species at 25% were not significantly different.

Total dry matter production for all the species decreased with increasing moisture stress. Reduction in biomass production due to moisture stress is well established (Pereira and Pallardy, 1989, Teskey and Hinckley, 1986). Reduction in growth is considered the principal effect of drought (Silva, 2010). The response to moisture stress results in the reduction of dry matter production (Greco and Cavagnaro, 2003, Rawat and Singh, 2000). The highest dry biomass was produced by *S. macrophylla* as this species has different morphology than the other two species, for example, large leaves and initial high shoot development. Both *A. nilotica* and *P. dulce* showed a similar reduction of dry matter production (Rawat and Singh, 2000). An investigation on relative growth rate (RGR) in future may be useful to shed more clarification on morphological traits. In this study, continuous monitoring of growth was not possible due to several limitations, including appropriate time, space and resources.

5. Conclusion

This study has presented the results of three contrasting agroforestry tree species under different water stress conditions. The moisture compensation strategies were varied among these species. In this context, both *A. nilotica* and *P. dulce* have suitable adaptation strategies to thrive in a low moisture regime at 25% SWC, compared with *S. macrophylla*.

Germination behaviour was markedly different between species and in response to water stress. *P. dulce* was well adapted to moisture stress during germination, with rapid onset under moist conditions and adequate germination success under all SWC treatments. Both *P. dulce* and *A.nilotica* achieved relatively low maximum germination percent, suggesting that these species "hedge their bets" by retaining a significant proportion of ungerminated seed even under good moisture conditions. *Swietenia macrophylla* in contrast was adapted to rapid and more complete germination under moist conditions, consistent with its recalcitrant seed classification.

Swietenia macrophylla was found to be intolerant of low moisture, whereas *A. nilotica* and *P. dulce* were comparatively efficient in coping with low moisture regimes by adjusting their growth behaviour. Although *P. dulce* displayed poorer survivability at low moisture (25% SWC), those seedlings that survived showed superior growth to *A. nilotica* under the same conditions.

The research highlights that further research is needed to evaluate the effect of water stress on agroforestry species in Bangladesh. The selection of species is vital to prevent mortality under stressed conditions and ensure food and livelihood security to the farmers in drought-prone areas. Being able to predict agroforestry species' germination and growth performance at different water-stressed conditions would be useful to select suitable species in drought-prone areas, especially to restore degraded and barren areas of Bangladesh through afforestation.

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Declaration of Competing Interest

The authors declare that there is no conflict of interest among them.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.envc.2021.100256.

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