RESEARCH ARTICLE

Germination and seedling growth responses of Sri Lankan grown Sesame/Thala (*Sesamum indicum* L.) for simulated drought conditions

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Abstract: The agriculture sector is often challenged by dry weather, thus a better understanding of growth responses of crops to changes in climate is imperative. However, drought responses of many economical crops are yet to be comprehensively studied. Therefore, this research was carried out to investigate the responses of 10 Sri Lankan grown sesame varieties/cultivars: *Uma*, *Malee*, *Idal*, *Pokuru*, Black-seeded sesame and its wild relatives, to reduced water availability during germination and seedling growth. Drought conditions were simulated in a laboratory with three different treatments [polyethylene glycol (PEG) 6000, mannitol and sodium chloride] at 0, - 0.25, - 0.5 and -1.0 MPa water potentials under complete randomised design with 10 replicates each having eight seeds per petri plate per variety/cultivar. The final germination percentage of sesame seeds after 10 days was calculated. Seedlings were further exposed to the same treatments and their root and shoot lengths were measured after 10 days. Germination was assessed using binary data analysis and the seedling data were subjected to ANOVA. Results revealed that the highest tension of PEG (-1.00 MPa) inhibited seed germination and the emergence of seedlings, while that of mannitol (-1.00 MPa) negatively affected seedling growth only ($p < 0.001$). It is concluded that sesame varieties/cultivars were drought susceptible at a tension of -1.00 MPa during germination and seedling development. Improved cultivars (*Uma* and *Malee*) showed to be more drought tolerant during germination and landraces (*Idal* and *Pokuru*) were the least susceptible to drought during seedling growth. Seedlings of Black₁, Wild₁, Wild₂, *Pokuru* and *Uma* varieties/cultivars developed morphological adaptations to display drought avoidance responses during the period of drought stress.

Keywords: Drought tolerance, germination, gingelly, seedling growth, sesame.

INTRODUCTION

With climate change, it is expected that drought conditions will increase in frequency and intensity in the coming years, severely affecting agriculture, especially rain-fed agriculture and threaten the food security of humans (IPCC, 2014). Effects of drought on crops are multiple and complex as they interfere with the composition, structure and function of plants from sub-cellular levels to ecosystem level depending on the severity of the drought regime, and the phenological and developmental stages of the crop (De Costa, 2004, 2010; Lambers *et al.*, 2008; Alqudah *et al.*, 2011). Drought responses of major crops such as rice, wheat, barley, sorghum, and maize have already been extensively researched (Harris *et al.*, 2007; Ali *et al.*, 2013; Odabas *et al.*, 2014; He *et al.*, 2016; Ramya *et al.*, 2016) and insights have been made to develop drought-resistant varieties. However, many other economical crops are yet to be comprehensively studied.

Sesame (*Sesamum indicum* L., Family Pedaliaceae) has been reported to be highly responsive to many environmental factors such as air temperature, salinity, heavy metals and soil moisture (Bor *et al.*, 2009) which

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affect its growth (reduction in length of shoots and roots, and biomass) and yield performance. Nevertheless, detailed studies on responses of sesame to environmental conditions are underestimated and reports are limited (Nath *et al.*, 2001; Olowe *et al.*, 2009).

Being the major rain-fed oil seed crop cultivated in Sri Lanka (Weeraratna & Weerasinghe, 2009), different sesame cultivars are grown in the island. For instance, white seeded sesame cultivars are mainly grown in the South eastern regions while black seeded cultivars are common in the North western parts of the country (Dissanayake *et al.*, 2017). Either white or black seeded sesame cultivars are cultivated in other parts of the country depending on the seed availability. *Pokuru* and *Idal* are the white seeded landraces found in cultivations in Sri Lanka. Limited cultivation of improved cultivars, namely, *Uma* (white seeded) and *Malee* (brown seeded) are also recorded in Hambantota district.

Despite the high international demand of sesame for oil, bakery and confectionary products, it is identified as an underutilised crop in Sri Lanka (Dissanayake *et al.*, 2017). Nevertheless, the Sri Lankan government has taken initiatives to expand sesame cultivation to reach zero imports by the year 2020 (Department of National Planning, 2010).

This study comparatively assessed the drought resistance of Sri Lankan grown sesame cultivars and its wild relatives through experiments conducted by simulating reduced water availability during seed germination, and seedling growth and establishment. We hypothesised that germination and seedling growth of sesame varieties/cultivars respond differently to water availability of the environment.

Osmotic stress is often simulated using osmotica such as polyethylene glycol (PEG), mannitol, sodium chloride (NaCl), sucrose and glucose in laboratory experiments (Mensah *et al.*, 2009; Boureima *et al.*, 2011; Bahrami *et al.*, 2012). PEG and mannitol are organic compounds not largely ionised in water, but mainly exert osmotic effects compared to NaCl, which is inorganic and ionised in water imposing a salinity effect in addition to the osmotic effect (Mensah *et al.*, 2009). PEG is non-toxic to plant cells and metabolism, hence, considered as a better osmoticum to study drought responses in laboratory experiments (Verslues *et al.*, 2006; Mensah *et al.*, 2009; Bahrami *et al.*, 2012).

Here, simulated drought stress was quantified with regard to the osmotic potential to identify varieties/

cultivars tolerant to drought during germination and seedling growth stages. It was assumed that the use of different osmotica will also reveal hints on how sesame could cope with salinity stress induced by NaCl.

METHODOLOGY

Plant material

Seed samples from 10 different sesame varieties/ cultivars were used. These included black seeded cultivars (Black₁ from Anuradhapura, Black₂ from Puttalam, Black₃ from Hambantota), black seeded wild varieties from the Plant Genetic Resources Centre (PGRC), Gannoruwa (Wild₁ - accession no. 002324 origin from Gampaha, Wild₂ - accession no. 008824 origin from Matale, Wild₃ - accession no. 001853 origin from Kandy), white seeded *Idal* (meaning broom) and *Pokuru* (meaning clusters) landraces from Hambantota, and *Uma* and *Malee* developed by the Grain Legumes and Oil Crops Research and Development Centre of the Department of Agriculture (DOA), Angunakolapelessa, Sri Lanka.

Germination and seedling growth experiment

Drought stress on the germination of sesame seeds was simulated at 29 °C and 12 h day/night conditions under complete randomised design with 10 replicates each having 8 seeds per petri plate per variety/cultivar. Treatments included osmotica: PEG 6000, mannitol and NaCl at -0.25, -0.5 and -1.0 MPa osmotic potentials selected upon results of a trial experiment conducted to simulate drought stress at water potential levels equivalent to -0.25, -0.5 and -1.0 MPa, respectively. Distilled water (0 MPa) was used as the control.

Having known the solute concentration, osmotic (solute) and water potentials exerted by a given solution can be expressed by the Van' Hoff equation (equation 1) (Ashraf & Abu-Shakra, 1978; Richards, 2005) and summing up of its components (equation 2) (Sanders & Arndt, 2012).

$$\text{Osmotic potential } (\psi_s) = -iCRT \quad \dots(1)$$

where i = number of particles the molecule makes in water, C = molar concentration (mol/L), R = pressure constant (0.0821 L atm/mol/K), and T = temperature in K

$$\begin{aligned} \text{Water potential } (\psi_w) + \text{pressure potential } (\psi_p) \\ = \text{osmotic potential } (\psi_s) \end{aligned} \quad \dots(2)$$

Thus, a range of water potential values and subsequent drought stress conditions could be imposed by a concentration gradient of an osmoticum.

Sesame seeds washed under running tap water for 20 min were placed on a Whatman filter paper soaked in 10 mL of treatment solution in petri plates (100 mm * 15 mm). Seeds were considered as germinated when the radical was approximately 5 mm long. Observations were recorded every 48 h within a 10-day period and the germinability (germination percentage) was calculated (McNair *et al.*, 2012).

Binary data analysis detected differences in germination at different drought stress (water potential) levels. Number of seeds germinated was converted to an odds value, i.e. the probability of germination for a treatment (P)/ probability that germination did not occur for the same treatment ($1 - P$) (Thattil *et al.*, 1999) and the effects were compared using the ratios, i.e. the ratio of the probabilities for germination for any two treatments being compared. When the odds ratio was significantly different from 1, the compared treatments were considered to differ significantly from each other (James *et al.*, 2003). Odds ratio for any treatment was compared against the response of the seeds in the control at full water availability (0 MPa), i.e. numerator was the odds in the treatment and denominator was the odds in the control. In order to test for interaction effects, the data were stratified by variety and post-hoc comparisons were done based on odds.

All germinated seeds of the 10 varieties/cultivars were separately transferred into a tray containing sterile sand, saturated with the respective treatment solutions for further growth. Root and shoot lengths of 10 developing seedlings of each variety/cultivar were measured after 10 days. Each seedling represented a replicate. The data were subjected to analysis of variance (ANOVA) to detect differences among drought stress (water potential) levels.

Data were analysed using Statistical Analysis System (SAS) software version 9.3 (SAS Institute, Cary, North Carolina, U.S.) and GraphPad Prism 6 (GraphPad Software, Inc., CA) was used for generating graphs. Logistic regression was followed with PROC LOGISTIC procedure to study the effect of osmotic treatments on germination response of seeds of 10 sesame varieties. Firth's penalised likelihood method was used to alleviate issues with quasi separation. During ANOVA, the mean separation of the parameters with significant differences was done by Duncan's multiple range test. Normal distribution was evaluated using the Shapiro-Wilk W test

and the data were transformed (to square root of root and shoot lengths) to meet the assumptions of ANOVA.

Drought tolerance

Drought tolerance of the tested varieties/cultivars was evaluated against tolerance indices, namely, reduction rates of germination and growth of seedlings following the formula (equation 3) given by Boureima *et al.* (2011).

$$\text{Reduction rate (\%)} = \left[1 - \frac{V_s}{V_p} \right] * 100 \quad \dots(3)$$

where V_s and V_p are the mean of the parameter under stressed and non-stressed conditions, respectively.

RESULTS AND DISCUSSION

Seed germination

A test of the full model against a constant-only model was statistically significant, indicating that the treatments and varieties reliably distinguished between germination responses ($X^2 = 5986$, $p < 0.001$ with $df = 99$) with a 93 % concordant value. Wald criterion demonstrated that the effect of treatment, varietal/cultivar difference and treatment variety/cultivar interactions were significant ($p < 0.001$).

Osmotic treatments had a significant effect ($p < 0.001$) on all sesame varieties/cultivars.

Black seeds (Black₁) showed a significant decrease in germination percentage with increased osmotic tension of PEG and mannitol (Figure 1a). Black₂ seeds did not germinate to any appreciable degree under any treatment (Figure 1b), while Black₃ seeds germinated well in all treatments except for PEG at -1.00 MPa (Figure 1c). Wild sesame seeds, especially Wild₁ and Wild₂, showed negative germination responses to osmotica, PEG and mannitol (Figure 1d, 1e, and 1f). Landraces *Idal* and *Pokuru* responded positively to mannitol and PEG (except for -1.00 MPa of PEG) and negatively to high tension of osmotic stress imposed by NaCl (Figure 1g and 1h). Seeds of *Uma* and *Malee* cultivars germinated well regardless of the treatment and were only affected at the highest tension of osmotic stress imposed by PEG (-1.00 MPa) (Figure 1i and 1j).

In general, Wild and *Idal* seeds showed lower germination percentages (less than 70 %) even in distilled water (Figure 1d, 1e, 1f and 1g). The low values of germination exposed to distilled water may

Figure 1: Effect of simulated water stress on germination percentage of sesame cultivars: Black₁ (a), Black₂ (b), Black₃ (c), Wild₁ (d), Wild₂ (e), Wild₃ (f), *Idal* (g), *Pokuru* (h), *Uma* (i) and *Malee* (j). Data are the mean germination percentages + standard error and the values with the same colour are not statistically different from the control at $p = 0.05$ level (based on odds ratios).

reflect the germination capacity of the seeds of Wild and *Idal* that were randomly selected from PGRC and a composite sample of seeds obtained from the farmers in Hambantota, respectively. Germination of seeds of the varieties/cultivars, except for *Uma* and *Malee*, was completely inhibited by a water potential of -1.00 MPa of PEG. At the end of 10-day period, germinated *Uma*, *Malee* and *Pokuru* seeds also did not complete shoot emergence at -1.00 MPa water potential imposed by PEG. Nevertheless, the radical continued to grow increasing the length of the roots.

Seedling establishment and growth

A two-way analysis of variance of square root of root length of seedlings exhibited a significant interaction between simulated osmotic treatments and variety/cultivar [$F(60,1053) = 3.29$, $p < 0.001$]. Both effects of osmotic treatments [$F(60,1053) = 76.04$, $p < 0.001$] and variety/cultivar differences [$F(60,1053) = 24.19$, $p < 0.001$] were significant. Thus, the effect of osmotic stress on seedling growth depended on the variety/cultivar. The means for the osmotic treatments were significantly different for Black₁ [$F(60,1053) = 21.30$, $p < 0.05$], Black₂ [$F(60, 1053) = 3.38$, $p > 0.05$], Black₃ [$F(60, 1053) = 11.54$, $p > 0.05$], Wild₁ [$F(60, 1053) = 2.07$, $p < 0.05$], Wild₂ [$F(60, 1053) = 10.86$, $p < 0.05$], Wild₃ [$F(60, 1053) = 3.23$, $p < 0.05$], *Idal* [$F(60, 1053) = 17.46$, $p < 0.05$], *Pokuru* [$F(60, 1053) = 9.51$, $p < 0.05$], *Uma* [$F(60, 1053) = 18.84$, $p < 0.05$] and *Malee* [$F(60, 1053) = 9.73$, $p < 0.05$]. The effects of different levels of osmotic stress (as indicated by the water potential) on root growth recorded 10 days after planting exhibited a significant reduction of sesame root growth with increased osmotic tension of mannitol (Figure 2a, 2b, 2c, 2e, 2g, 2h, 2i, and 2j).

The wild varieties hardly survived in the mannitol solutions (Figure 2d and 2f). Increasing the osmotic tension of NaCl also reduced root elongation in Black₃, Wild₁ and *Uma* sesame seedlings (Figure 2c, 2d, and 2i). In contrast, increasing tension of PEG induced root growth of Black₁, Wild₁, Wild₂, *Pokuru* and *Uma* seedlings compared to that of the control (Figure 2a, 2d, 2e, 2h, and 2i).

Two-way analysis of variance of square root of shoot length of seedlings indicated a significant interaction between simulated osmotic treatment and variety/cultivar [$F(60,1053) = 10.08$, $p < 0.001$]. Both effects of osmotic treatment [$F(60,1053) = 108.54$, $p < 0.001$] and variety/cultivar [$F(60,1053) = 113.70$, $p < 0.001$] were significant. The means for the osmotic treatments were significantly different for Black₁ [$F(60,1053) = 35.83$,

$p < 0.05$], Black₂ [$F(60,1053) = 4.03$, $p > 0.05$], Black₃ [$F(60,1053) = 16.32$, $p > 0.05$], Wild₁ [$F(60,1053) = 3.08$, $p < 0.05$], Wild₂ [$F(60,1053) = 6.23$, $p < 0.05$], Wild₃ [$F(60,1053) = 4.83$, $p < 0.05$], *Idal* [$F(60,11053) = 27.48$, $p < 0.05$], *Pokuru* [$F(60,1053) = 31.05$, $p < 0.05$], *Uma* [$F(60,1053) = 35.93$, $p < 0.05$], and *Malee* [$F(60,1053) = 25.73$, $p < 0.05$].

Growth performance of the shoots in response to osmotic solutions recorded 10 days after planting indicated a low growth increment in white, black and brown seeded sesame varieties/cultivars treated with high osmotic tension provided by mannitol (Figure 3a, 3b, 3c, 3e, 3g, 3h, 3i, and 3j).

Wild seedlings did not survive in mannitol (Figure 3d and 3f). Lower osmotic tensions of NaCl, induced shoot growth in Black₁, Black₃, Wild₂, *Pokuru*, *Uma*, and *Malee* (Figure 3a, 3c, 3e, 3h, 3i, and 3j). Seeds of Black₂ did not germinate in distilled water (Figure 1b) possibly due to the germination capacity of the seeds, which were also randomly selected from a composite seed sample and hence, no further measurements were taken.

Drought tolerance

Among the treatment regimes, the highest tension of PEG (-1.00 MPa) significantly lowered germination of sesame seeds (Figure 1) and the highest tension of (-1.00 MPa) mannitol negatively affected the growth of sesame seedlings (Figures 2 and 3). Reduction rates of germination and seedling growth calculated for -1.00 MPa PEG and -1.00 MPa mannitol, respectively (Table 1) indicated that seed germination of wild (Wild₁, Wild₂, Wild₃), black (Black₁, Black₂, Black₃) and *Idal* sesame was completely (100 %) reduced by -1.00 MPa PEG, whereas *Uma* and *Malee* showed a relatively low germination reduction (88 % and 86 %, respectively), suggesting high tolerance of *Uma* and *Malee* compared to the other tested varieties/cultivars.

Water potential directly indicates the availability of water for the survival of living cells. In most instances in a tropical climate, at field capacity where soil water is abundant, ψ_w remains as -0.033 MPa, providing a favourable condition for optimum crop growth. When ψ_w hits the permanent wilting point generally considered to be -1.5 MPa, the crops are severely stressed and irreversibly damaged (Elkheir *et al.*, 2016).

Our results showed that none of the seedlings of Wild₁ and Wild₃ sesame survived in -1.00 MPa imposed by mannitol indicating that they were highly susceptible

Figure 2: Effects of different osmotic treatments on root growth of sesame seedlings: Black₁ (a), Black₂ (b), Black₃ (c), Wild₁ (d), Wild₂ (e), Wild₃ (f), Idal (g), Pokuru (h), Uma (i) and Malee (j). Data represent the mean and standard error of 10 replicates. Bars that share a common letter are not significantly different by Duncan's multiple range test at 95 % confidence interval.

to drought during seedling growth. It was not possible to calculate the reduction rate for Black₂, as none of the seedlings survived in the control. Seedlings of landraces *Pokuru* (40 %) and *Idal* (58 %) were shown to be the most tolerant to root growth although moderate reductions in

shoot growth (62 and 60 %, respectively) were observed. Shoot growth of Black seeded varieties (Black₁ – 48 % and Black₃ – 44 %) and *Uma* (44 %) were least affected by mannitol. Wild₂, Black₁, Black₃, *Uma* and *Malee* plants were moderately drought tolerant to root growth

Figure 3: Effects of different osmotic treatments on shoot growth of sesame seedlings: Black₁ (a), Black₂ (b), Black₃ (c), Wild₁ (d), Wild₂ (e), Wild₃ (f), *Idal* (g), *Pokuru* (h), *Uma* (i) and *Malee* (j). Data represent the mean and standard error of 10 replicates. Bars that share a common letter are not significantly different by Duncan's multiple range test at 95 % confidence interval.

(72, 64, 64, 78 and 77 %, respectively).

Similarly, the reduction of germination of all varieties/cultivars by -1.00 MPa imposed by PEG can be attributed to limited or no water uptake during germination under decreased water potential conditions, thus no seeds completed seedling emergence.

Regardless of the source of water potential, results of the germination and seedling growth experiments showed that sesame varieties/cultivars were drought susceptible at an osmotic tension of -1.00 MPa during germination and seedling growth. *Uma* and *Malee* were shown to be the most drought tolerant cultivars at the germination stage. They also showed moderate drought tolerance during seedling growth. *Idal* and *Pokuru* were moderately drought tolerant during germination and highly tolerant during seedling growth. Wild sesame plants were highly sensitive and intolerant to water deficit conditions at times of germination and seedling growth.

Biomass partitioning of roots and shoot growth provides a functional balance of growth. Shoot growth depends on the water absorbed from the root, whereas root growth depends on the supply of photosynthates from the shoot. At times of drought stress when shoot expansion becomes limited, accumulated photosynthates are translocated to the root allowing it to expand for search of soil water. Plants that increase root depth, root to shoot ratio and maintain water potential above that of the environment are termed as 'Water Spenders' (Bodner *et al.*, 2015) and it is a morphological adaptation that plants develop to avoid drought stress by optimizing water uptake (Farooq *et al.*, 2009, 2012). Seedlings of *Black₁*, *Wild₁*, *Wild₂*, *Pokuru* and *Uma* were capable of developing deep root systems under drought stress

(Figure 2a, 2d, 2e, 2h, 2i and Table 2) in favour of maximising its water absorption capacity to overcome drought stress at the seedling stage.

The order of effects produced by different osmotica on germination was PEG > mannitol > NaCl where no seedlings emerged at -1.00 MPa PEG treatment. The order of effects on seedling growth was mannitol > PEG > NaCl, hence, PEG and mannitol had high osmotic influence compared to that of NaCl. This observation is in agreement with the claim made by Luan *et al.* (2014) that, compared to PEG, NaCl had a less inhibitory influence on the germination of sunflower seeds, another oilseed crop. However, findings of a similar experiment carried out by Mensah *et al.* (2009) in Nigeria showed an order

Table 1: Comparison of reductions in germination and root and shoot length of sesame.

	RPG (%)	RPSR (%)	RPSS (%)
<i>Black₁</i>	100	64	48
<i>Black₂</i>	100	NS ^a	NS ^a
<i>Black₃</i>	100	64	44
<i>Wild₁</i>	100	100	100
<i>Wild₂</i>	100	72	60
<i>Wild₃</i>	100	100	100
<i>Idal</i>	100	58	62
<i>Pokuru</i>	95	40	60
<i>Uma</i>	88	77	44
<i>Malee</i>	86	78	64

^a NS - seedlings did not survive to calculate reduction percentage.

RPG - reduction rate of germination; RPSR - reduction percentage of seedling root length; RPSS - reduction percentage of seedling shoot.

Table 2: Effects of different osmotic solutions on shoot:root of the seedlings

	Control	NaCl (MPa)			PEG (MPa)		Mannitol (MPa)		
	0 (MPa)	-0.25	-0.5	-1.0	-0.25	-0.5	-0.25	-0.5	-1.0
<i>Black₁</i>	1.39	1.52	1.11	1.42	0.99	0.66	0.83	1.97	1.80
<i>Black₂</i>	-	1.03	0.68	-	1.66	0.57	1.42	1.53	0.93
<i>Black₃</i>	0.73	1.27	1.21	1.65	0.73	0.67	0.81	1.47	1.04
<i>Wild₁</i>	0.43	0.51	0.51	-	0.40	0.17	-	-	-
<i>Wild₂</i>	0.49	0.51	0.53	1.27	0.24	0.15	0.87	-	0.64
<i>Wild₃</i>	0.65	0.40	0.47	1.05	0.97	-	-	-	-
<i>Idal</i>	1.12	1.24	1.22	1.41	0.61	0.49	0.60	0.58	0.82
<i>Pokuru</i>	1.39	1.18	0.92	1.33	1.01	0.57	0.72	0.62	0.87
<i>Uma</i>	0.87	0.98	1.66	-	0.72	0.40	0.52	0.55	1.97
<i>Malee</i>	1.04	0.91	1.31	0.88	0.91	0.60	0.62	0.58	1.64

of potency of NaCl > Glucose > PEG on sesame seed germination, which can be attributed to the susceptibility to salinity rather than drought susceptibility. Although NaCl was imposing salinity stress in the present study, germination of sesame seeds would have been more vulnerable to osmotic/drought stress than salinity stress. Similarly, observations on *Idal* and *Pokuru* cultivars indicated their vulnerability to salinity stress during germination. Black₃ and Wild₁ also showed signs of vulnerability to salinity stress during seedling growth as imposed by NaCl at -1.00 MPa. Induced seed germination and shoot growth with lower osmotic potentials of NaCl could possibly be due to its Na⁺ and Cl⁻ ions that can mobilise through cell membranes which could, in turn, lower cellular water potential and increase water uptake (Luan *et al.*, 2014). Conversely, these authors have also declared that higher osmotic potential of NaCl can cause a toxic effect on germination and seedling growth. Mensah *et al.* (2009) also provided evidence that seed germination and seedling growth of sesame are negatively affected by NaCl at an osmotic potential of -0.5 MPa. A previous study conducted by Ramírez *et al.* (2007) on sesame demonstrated that there is a profound difference in germination percentages of various sesame genotypes in response to increased salinity stress.

Although it was presumed that PEG and mannitol would affect germination and seedling growth in the same way, in this study, mannitol showed only positive or neutral effects on sesame seed germination while PEG negatively influenced seed germination. Conversely, mannitol negatively affected seedling (both root and shoot) growth whereas PEG induced root growth of sesame seedlings. While working on wheat, Almansouri *et al.* (2001) also showed that mannitol had no effect on seed germination but negative significant effects on seedling length. Similar to NaCl, mannitol is a penetrating solute that decreases internal cellular water potential and facilitates osmotic water uptake inducing germination. Therefore, mannitol does not impose any inhibitory effect on seed germination. However, reduced seedling growth at the higher osmotic potential of mannitol is unexpected unless it is hypothesised that mannitol induces mild toxic effects at higher concentrations as shown by NaCl in the study conducted by Luan *et al.*, (2014). Mannitol is a form of reduced sugar mannose that is generally distributed in plant cells. In response to drought and salinity stress, it is evident that mannitol is accumulated in plant cells to act as osmoprotectant and antioxidant (Patel & Williamson, 2016). Hence, there should be another mechanism which explains the reducing effect of mannitol on sesame seedlings. By working on cucumber and pea seedlings, Stahlberg and Cosgrove (1997) demonstrated that mannitol had negative effects

on the growth of cucumber seedlings whereas no effect was recorded on pea seedlings. Further, these authors confirmed that mannitol was not penetrating into root cells of the seedlings and the reduction in growth rate of cucumber seedlings was due to the mannitol induced reduction in xylem pressure.

Mensah *et al.* (2009) discovered that an osmotic pressure value of -0.5 MPa of PEG reduced germination and radicle development of Nigerian sesame seeds with no shoot development. Similarly, Bahrami *et al.* (2012) showed that germination and seedling growth of sesame cultivars in Iran were reduced by PEG 6000 at 6 bar (-0.6 MPa), whereas in the present study sesame plants showed such responses at comparatively lower water potential/higher osmotic stress (-1.00 MPa). Increase in turgor pressure in embryo cells by accumulating solutes within these cells overcomes the resistance of surrounding tissues of the seeds for radicle penetration (Welbaum *et al.*, 1998). For instance, the accumulation of amino acids in embryos is evident during germination of lettuce seeds (Welbaum *et al.*, 1998). A similar mechanism would have allowed Sri Lankan sesame seeds to germinate in a water limited environment by facilitating water uptake through osmosis. High tolerance of Belgian sesame genotypes exposed to osmotic stress severely affected germination and seedling growth at levels greater than -1.00 MPa (Boureima *et al.*, 2011). The differences in tolerable limits in osmotic potential values could be due to the variability in tolerance in genotypes being tested in these experiments. As in this study, findings of both Boureima *et al.* (2011) and Bahrami *et al.* (2012) also indicated significant differences in response patterns among different sesame genotypes.

Drought causes severe damages to crops and livelihoods. Nearly half of the crop damages recorded from 1974 to 2008 in Sri Lanka was due to drought (Desinventer, 2012). Agricultural production was severely affected by drought during the *Maha* season in 2014 (World Food Programme, 2014). The entire dry zone is highly vulnerable to drought during *Yala* season (March to August) while the extreme regions in the North western and South eastern parts of the country are prone to severe drought conditions in *Maha* season (September to February) (Chithranayana & Punyawardena, 2009). With increased events of drought, development of high yielding crops with drought tolerance has been suggested as one of the drought adaptation strategies (Eriyagama *et al.*, 2010; World Food Programme, 2014). Therefore, it will be best to adapt for drought-tolerant crops in the drought-prone regions and sesame can be suggested as a suitable crop to cultivate in drought prone areas as it is mainly grown in the dry zone of Sri Lanka. There

are sesame varieties that can tolerate drought stress as high as -1.00 MPa during germination and seedling growth. In response to simulated drought conditions in the field, Dissanayake *et al.* (2016), and Dissanayake and Ranwala (2017) reported that sesame expresses versatile morphological adaptations to survive drought. Less inhibitory influence by the salinity effect of NaCl indicates the salinity tolerance of Sri Lankan sesame varieties/cultivars in general. This ability to tolerate salinity stress can also be considered as an added advantage in selecting sesame as a potential crop for the future.

CONCLUSION

Different sesame varieties/cultivars responded differently to PEG, mannitol and NaCl treatments of simulated drought stress. Improved cultivars (*Uma* and *Malee*) were shown to be the most drought tolerant during germination while landraces (*Idal* and *Pokuru*) were the most tolerant to drought stress at the seedling stage. Wild sesame varieties were highly sensitive to water deficit during germination and seedling growth. These findings on varietal resilience to drought stress are of immense importance for farmers, plant breeders and scientific research. This work also reflects the pressing need to conserve the genetic diversity of the drought-tolerant sesame landraces and further crop improvements to strengthen their drought-tolerant traits.

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