Pak. J. Bot., 48(2): 439-446, 2016.

SEED SIZE EFFECTS ON THE RESPONSE OF SEEDLINGS OF *ACACIA ASAK* (FORSSK.) WILLD. TO WATER STRESS

EL ATTA, H.A[*]., AREF, I.M. AND AHMED A.I

Department of Plant Production, King Saud University, Postal code: 11451, Riyadh, P.O. Box 2460, Saudi Arabia
[*]*Corresponding author's email: hmabu@ksu.edu.sa*

Abstract

Dry tropical forests are characterized by unpredictable spells of drought and climate change. Saudi Arabia mostly falls within the arid zone and some few scattered areas fall in the semiarid zone mainly in the South Western region. Rainfall is sparse and with sporadic distribution. Drought is the most critical factor for restoration of the tree cover. Within a tree, seeds vary in size from large to small seeds. Although several researchers have studied the effect of within species variation in seed size on seedlings growth parameters, however there is a lack of knowledge regarding the effect of seed size on stress tolerance (Khurana and Singh 2000). We assumed that seedlings grown from different seed sizes from the same tree species may influence their response to water stress. Seeds of *Acacia asak* (Forssk.) Willd. were categorized into large, medium and small seeds on the basis of the seed weight. Seedlings from the three seed sizes were grown in potted soil and subjected to 5 levels of field water capacity (FC) (100, 75, 50, 25 and 15%) in the greenhouse. The objective was to evaluate the response of seedling grown (from different seed sizes) to water stress and to understand the acclimation of seedlings to water stress. Water stress significantly reduced RWC, leaf area, and shoot length, fresh and dry weight. Significant correlations between growth parameters and water stress level were recorded. Seedlings from large seeds were heavier and comparatively less affected by drought compared to seedlings from smaller seeds. In all seedlings root length increased significantly and more biomass was allocated to roots than to shoots. However, at severe water stress (15% FC) no significant differences were reported between the three seedling categories. Therefore, raising of seedlings from large seeds is more appropriate for tree restoration programs under drought conditions.

Key words: Seed size; Water stress; Acclimation; Acacia asak.

Introduction

Tree seedlings in semi-arid and arid tropics have been challenged with climate change especially fluctuations and scarcity of rainfall. Under such conditions the ability of tree seedlings for acclimation is crucial for their survival (Matyssek *et al*., 2010; Pretzsch & Dieler, 2010). Changing maternal environmental conditions forced trees to produce variable seed mass (Foster, 1986; Hammond & Brown, 1995). Several investigators reported that seed size affected germination and seedling growth (Walters & Reich, 2000; Paz & Martinez Ramos, 2003; Iortsuun *et al*., 2008). Seedlings originated from large seeds were taller and produced greater biomass compared to those from smaller seeds (Khan, 2004). Nevertheless, seedlings from smaller seeds had more RGR (relative growth rate) (Paz & Martinez Ramos, 2003). Biomass allocation was more in large seeded seedlings than in small seeded seedlings (Yanlong *et al*., 2007). One of the indicators of forest tree seeds quality is the seed size (Moleele *et al*., 2005). Generally, seed mass has been very much linked with seedling performance (Castro *et al*., 2006). Large Seedlings originated from large seeds were capable to withstand unfavorable environmental conditions longer than those from small seeds (Ovcharov, 1977; Khera *et al*., 2004). This was attributed to the greater food reserves in large seeds (Fenner, 1985). Therefore, knowledge of the effect of seed mass on growth and survival of seedlings is of paramount importance for sound forest management that ensures successful restoration of degraded forests (Sa´nchez-Vela´squez *et al*., 2004; Martı´nez-Garza *et al*., 2005). Several effects of water stress on seedlings were recognized e.g. deformed foliage, little shoot growth, increased root/ shoot ratio, water potential and decreased leaf area (Buckley, 1982; Lloret *et al*., 1999; Pang *et al*., 2011). One of the most important plant acclimations to water stress is the increase in root/shoot ratio in order to enable the roots to grow deeper and spread more to maximize resources absorption especially water. Seedlings of *Pinus contorta* increased root/shoot ratio when water stressed (Nikolova *et al*., 2011). Alterations in root/shoot ratio was attributed to changes in biomass allocation to roots and shoots due to water stress (Olivas-Garcia *et al*., 2000; Panek & Goldstein, 2001). Water stress caused 100% mortality of small seedlings and 63-75% of large seedlings (Pinto *et al*., 2012).

Several investigators have reported that low soil fertility and drought stress enhanced biomass allocation to roots (Axelson & Axelson, 1986; Linder & Axelson, 1982; Murphy & Lugo 1986). Root/shoot ratio increased significantly in spruce under drought conditions (Clemensson-Lindell & Persson, 1993). Although increased root/shoot ratio is an important tool for soil resources utilization, however it is at the expense of carbon gain for photosynthesis and this may lead to a reduction in plant growth (Nielsen *et al*., 2001; Ho *et al*., 2005). However, the increased root/shoot ratio is sometimes controversial as it increased under water stress in the lab and decreased in the green house in *Brassica napus* (Benincasa *et al*., 2013). Although several researchers have studied the effect of within species variation in seed size on seedlings' growth parameters, however there is a lack of knowledge regarding the effect of seed size on stress tolerance (Khurana & Singh, 2000).

Materials and Methods

Raising of seedlings: Ripe pods of *Acacia asak* (Forssk.) Willd. were collected randomly from ten trees in Al Madinah (24°89´N, 39°16´E) in Saudi Arabia. The pods were broken by hand and only intact and healthy seeds were collected. About 1500 seeds were collected and dried to constant weights. Seeds were weighed with an electronic balance and divided into 3 non-overlapping sizes: small (0.12-0.16 mg), medium (0.17-0.21 mg) and large seeds (> 0.21). Hundred seeds from each size were soaked in in H_2SO_4 (98%) for 60 minutes, rinsed several times in running tap water and dried. Twenty seeds from each seed size class were transferred to Petri dishes (9 cm) containing moistened 3 Whatman filter paper No. 1. Petri dishes were incubated at 30 ± 1 °C. Emergence of the radicle was considered as an indicator to germination. After 2 weeks uniformly sized seedlings in each category were transplanted to moist soil (clay: sand, 1:1 v/v) in pots (1500 cm³) as 2 plants /pot. The pots were kept in a glasshouse (29-36 °C). The experiment was replicated 50 times/seed size. Prior to water stress application, seedlings were watered regularly for 3 weeks (Khurana & Singh, 2000). Seedlings from large, medium and small seeds were refed to henceforth as LS, MS and SS, respectively. Seedlings were then subjected to 5 levels of watering: 100% field water capacity (FC), 75%, 50%, 25% and 15 %. The experiment was replicated 10 times/seedling category/FC. Another set of identical pots were weighed every other day and water was added as required to maintain the five levels of field capacity.

Leaf relative water content (RWC): RWC was measured every 2 weeks after commencement of water stress experiments using 2nd, 3rd and 4th leaf/treatment/replicate. Leaves were weighed immediately (leaf fresh weight) after detachment and the petioles were immersed in water in beakers overnight to attain full turgidity. Leaves were then dried in an oven at 80 ± 2°C for 24 h to obtain dry weight. RWC was calculated according to Morgan (1984) as follows:

$$RWC = [(M_f - M_d)/(M_t - M_d)-1] \times 100$$

where: M_f is the leaf fresh weight; M_t is the turgid weight and M_d is the dry weight .

Leaf area: Leaf area was measured on 5 leaves/ treatment/ replicate after 6 months using a computer software (Area scan 2 MFC Application ver. 1001).

Shoot and root measurements: After 6 months all seedlings were harvested and the following growth parameters were measured: shoot and root length; shoot and root fresh and dry weights and root/shoot ratio.

Statistical analysis: The experimental design was a complete randomized block design (CRBD). Data were analyzed between seedling sizes by analysis of variance (ANOVA) and means were separated by the least significant difference (LSD) at P= 0.05 using SAS computer statistical package ((SAS, 1997). Analysis of data within individual seedling size was done by correlation analysis using SAS.

Results

RWC: Generally, RWC decreased with increased water stress in all treatments. LS and MS seedlings had significantly (P=0.01) more RWC than SS (Table 1). At FC 100% RWC in LS and MS seedlings was not significantly different. However, at severe water stress (FC=15%) there were no significant differences in RWC between all seedling sizes (Table 1). Significant negative correlations were recorded between water stress level and treatments (r= 0.966, P=0.001; r= 0.984, P=0.001 and r= 0.961, P=0.001 for LS, MS and SS, respectively) (Fig. 1). RWC was reduced at 15% FC from 86.8 % to 59.3%; 86.5% to 59.5% and 83.0% to 58.3% in LS, MS and SS seedlings, respectively (Table 1).

Leaf area: Leaf area was significantly more in LS as compared to MS and SS seedlings with the exception of FC 25% where leaf area was not significantly different between LS and MS (Table 1). At FC 15% all seedling categories showed no significant differences in leaf area. There were significant negative correlations between LA and water stress level (r= 0.901, P=0.01; r= 0.881, P=0.01 and r= 0.950, P=0.01 for LS, MS and SS seedlings, respectively) (Fig. 2). Leaf area was reduced considerably at FC 15% as compared to control. The reductions were from 3.7 to 1.3(64.9%); 3.4 to 2.3 (61.8%) and 2.6 to 1.1 (cm³) (57.8%) in LS, MS and SS, respectively (Table 1).

Table 1. Mean RWC (%) and leaf area of *A. asak*.

FC (%)	LS	MS	SS	R^2	F_p	$LSD_{0.05}$
	RWC (%)					
100	86.8a*	86.5a	83.0b	60	0.01	2.7
75	84.0a	81.8b	81.6b	64	0.001	1.5
50	77.0a	67.5b	64.8c	94	0.001	2.5
25	67.0a	61.0b	60.5b	72	0.001	3.4
15	59.3a	59.5a	58.3a	0.15	>0.05	1.9
	Leaf area					
100	3.7a	3.4b	2.6c	95	0.001	0.2
75	3.4a	2.7b	1.9c	95	0.001	0.3
50	3.0a	2.9a	1.5b	90	0.001	0.5
25	2.5a	2.2a	1.5b	66	0.01	0.54
15	1.3a	1.3a	1.1a	36	>0.05	0.28

FC= Field capacity; LS= Large seedlings; MS= Medium seedlings; SS= Small seedlings; *Fp*= F value probability; LSD= Least significant difference at P = 0.05

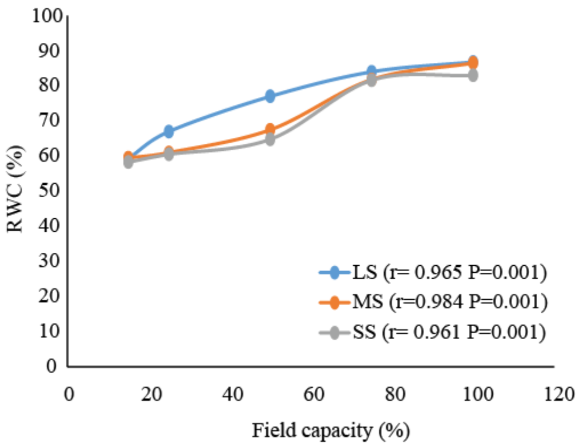

Fig. 1. Effect of water stress on relative water content of *A. asak* seedlings.

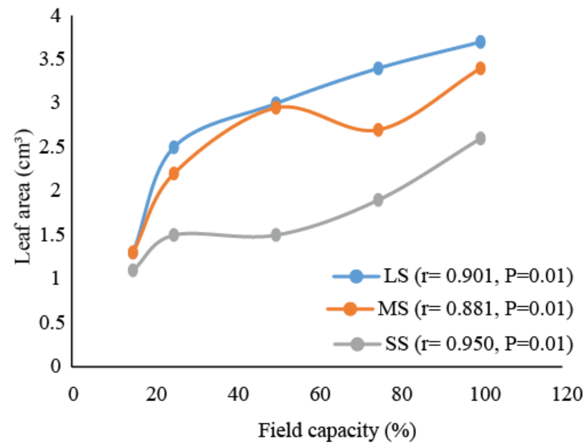

Fig. 2. Effect of water stress on leaf area of *A. asak* seedlings.

Table 2. Mean shoot and root length of *A. asak* seedlings.

FC%	LS	MS	SS	R^2 (%)	F_p	LSD $_{0.05}$
			Shoot length (cm)			
100	26.5a	23.3a	15b	70	0.01	5.8
75	25.5a	14.3b	14.3b	62	0.01	5.1
50	18.0a	13.3b	13.5b	74	0.001	2.8
25	19.5a	12.0b	12.3b	57	0.01	5.1
15	15.3a	11.0b	10.8b	50	0.01	3.5
			Root length (cm)			
100	35.7a	24.5b	19.0c	52	0.01	23.7
75	36.8a	23.5b	22.8b	74	0.001	8.0
50	38.5a	25.8b	24.3b	55	0.01	10.7
25	43.5a	32.8b	29.7b	84	0.001	5.2
15	51.0a	36.3b	34.8b	2.0	>0.05	12.1

Means in a row followed by the same letter are not significantly different at P=0.05

Shoot and root length: Shoot length decreased with increasing water stress. Generally, LS seedlings showed significantly more shoot length as compared to MS and SS seedlings. However, at FC=100% and FC=15% the shoot length was not significantly different between LS and MS (Table 2). The reductions in shoot length were 42.3%; 52.8% and 28% in LS, MS and SS seedlings, respectively. It is noteworthy that the reduction in SS shoot length was almost 2 folds less than in LS and MS. As water stress level increased, shoot length decreased significantly: r= 0.917, P=0.01; r=0.890, P=0.01 and r= 0.958, P= 0.01 in LS, MS and SS seedlings, respectively (Fig. 3). Root length increased significantly with increasing water stress level. Root length of LS consistently significantly increased more than MS and SS seedlings (Table 2). However, at severe water stress (FC= 15%) there were no significant differences in root length between the three sizes of seedlings. Significant correlations between root length and water stress level were recorded: r= - 0.887 (P=0.01); r= - 0.891 (P= 0.01) and r= - 0.958 (P=0.01) in LS, MS and SS seedlings, respectively (Fig. 4).

Shoot and root fresh weight: Generally, shoot fresh weight was much higher in LS and MS than in SS seedlings. However, as the FC decreased to 25 and 15% no significant differences were recorded between treatments (Table 3). As water stress level increased, shoot fresh weight decreased in all treatments: r= 0.957 (P= 0.01); r= 0.987 (P= 0.001) and r= 0.886 (P= 0.01) in LS, MS and SS seedlings, respectively (Fig. 5). In contrast root fresh weight increased with increasing water stress. In control no significant differences were recorded between treatments (Table 3). Nevertheless, at 75-15% FC LS produced significantly more root fresh weight. Water stress was significantly correlated with root fresh weight in all treatments: r= 0.897 (P= 0.01); r= 0.859 (P= 0.05); and r= 0.874 (P=0.05) in LS, MS and SS seedlings, respectively (Fig. 6).

Shoot and root dry weight: Shoot dry weight was more in LS as compared to MS and SS seedlings at 100 and 75% FC, however at 25 and 15% FC there were no significant differences in shoot dry weight between treatments (Table 4). Generally shoot dry weight decreased with increasing water stress: r= - 0.997 (P= 0.001); r= 0.992 (P= 0.001) and r= 0.950 (P=0.01) in LS, MS and SS seedlings, respectively (Fig. 7). In contrast, root dry weight increased significantly with increasing water stress in all seedlings: r= - 0.944 (P= 0.01); r= - 0.910 (P= 0.01), r= - 0.998 (P= 0.001) in LS, MS and SS, respectively. Nevertheless, in SS the root dry weight decreased significantly with increasing water stress (r= 0.985, P= 0.001) (Fig. 8).

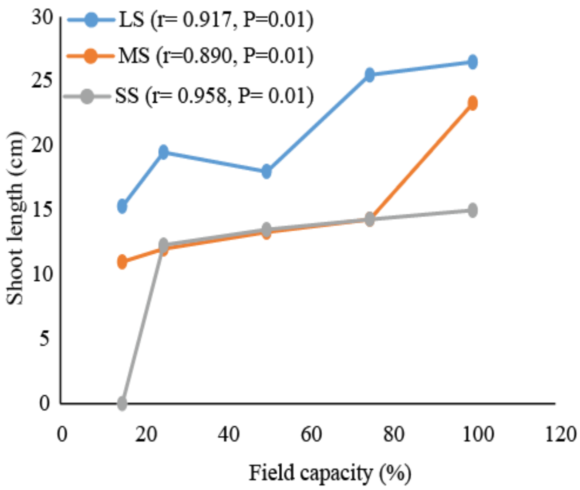

Fig. 3. Effect of water stress on shoot length of *A. asak* seedlings.

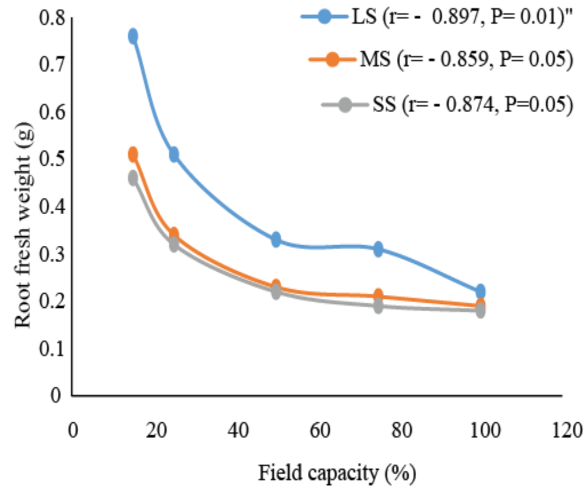

Fig. 6. Effect of water stress on root fresh weight of *A. asak* seedlings.

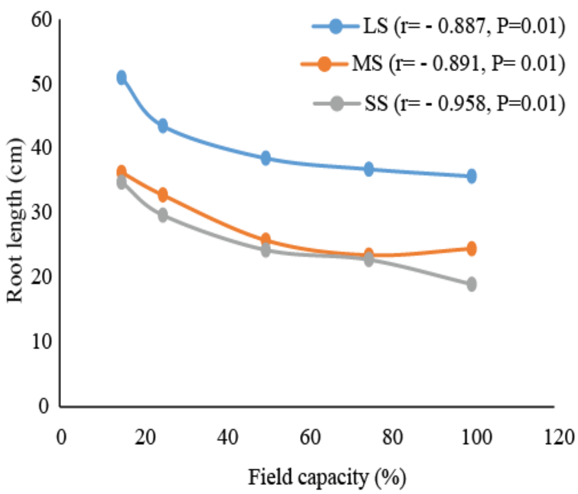

Fig. 4. Response of root length of *A. asak* seedlings to water stress.

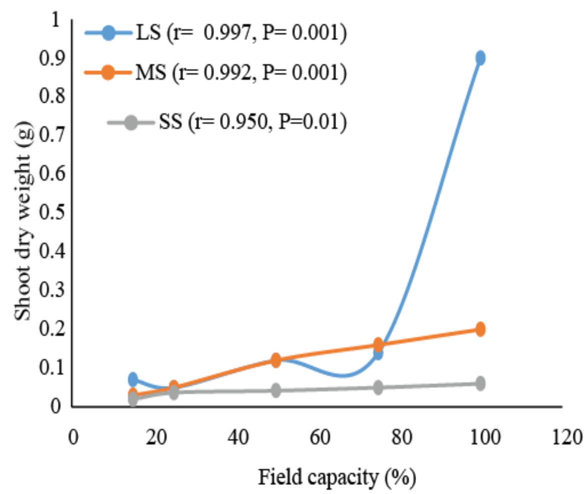

Fig. 7. Response of shoot dry weight of *A. asak* seedlings to water stress.

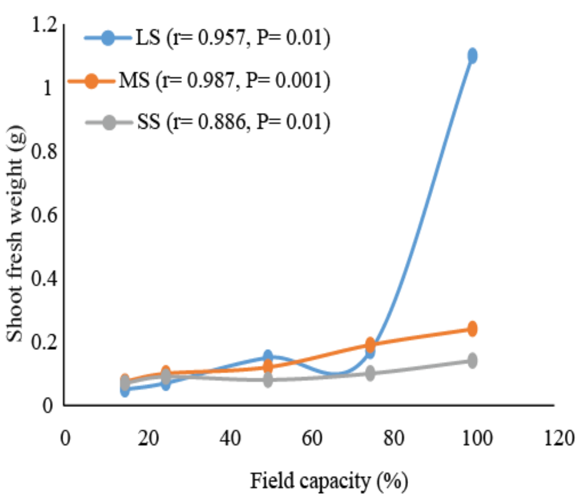

Fig. 5. Response of shoot fresh weight of *A. asak* seedlings to water stress.

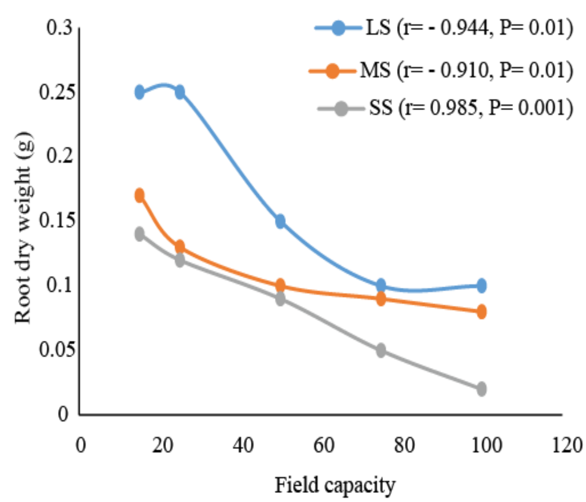

Fig. 8. Response of root dry weight of *A. asak* seedlings to water stress.

Table 3. Shoot and root weight of *A. asak*.

FC (%)	LS	MS	SS	R^2	F_p	LSD $_{0.05}$
			Shoot fresh weight (g)			
100	1.1a	0.24b	0.14c	85	0.001	0.05
75	0.17a	0.19a	0.10b	52	0.01	0.07
50	0.15a	0.12ab	0.08b	65	0.001	0.07
25	0.07a	0.10a	0.09a	14	>0.05	0.09
15	0.05a	0.075a	0.07a	11	>0.05	0.06
			Root fresh weight (g)			
100	0.22a	0.19a	0.18a	67	0.001	0.17
75	0.31a	0.21b	0.19b	57	0.01	0.10
50	0.33a	0.23b	0.22b	48	0.05	0.9
25	0.51a	0.34b	0.32b	87	0.001	0.01
15	0.76a	0.51c	0.46c	75	0.01	0.25

FC= Field capacity; LS= Large seedlings; MS= Medium seedlings; SS= Small seedlings; *Fp*= F value probability; LSD= Least significant difference at P = 0.05

Table 4. Mean Shoot and root dry weight of *A. asak* seedlings.

FC%	LS	MS	SS	R^2 (%)	F_p	LSD $_{0.05}$
			Shoot dry weight (g)			
100	0.9a	0.2b	0.06c	54	0.01	0.06
75	0.14a*	0.16b	0.05c	95	0.001	0.11
50	0.12a	0.12a	0.042b	60	0.01	0.07
25	0.05a	0.05a	0.037a	20	>0.05	0.05
15	0.07a	0.03b	0.02b	31	>0.05	0.04
			Root dry weight (g)			
100	0.1a	0.08a	0.02c	75	0.001	0.06
75	0.1a	0.09a	0.05b	86	0.001	0.04
50	0.15a	0.1b	0.09c	47	0.05	0.01
25	0.25a	0.13b	0.12b	20	>0.05	0.08
15	0.25a	0.17b	0.14b	1.0	>0.05	0.03

Means in a row followed by the same letter are not significantly different at P=0.05

Discussion

Generally, water stress had significantly reduced growth parameters of *A. asak* seedlings subjected to five levels of FC. These reductions were significantly correlated with water availability. However, root length and root fresh and dry weights increased with water stress. Seedlings from large, medium or small seeds had a considerable effect on the response of seedlings to various water stress intensities. Growth parameters were significantly greater in LS > MS> SS at 100, 75 and 50% FC, respectively. Nevertheless, LS and MS; and MS and SS responded similarly to water stress with regard to some growth parameters. Growth parameters of all categories of seedlings were all affected at higher water stress intensity (25 and 15% FC). These results are in agreement with those of Khurana & Singh (2000) who reported that seedlings from large seeds were heavier and had more leaf area enabling them to tolerate more water stress compared to seedlings from smaller seeds. Several investigators have reported significant reductions in the overall growth of tree seedlings in response to water stress such as *Hopea griffithii, Vatica maingayi* (Burslem *et al*., 1996); *Acacia nilotica* (Wilson & Witkowski, 1998), *Albizia procera* (Khurana & Singh, 2000); and *Acacia ehrenbergiana* and *Acacia tortilis* (El Atta *et al*., 2012). In the present study RWC was reduced in all seedling categories as a result of water stress. At 75 and 50% FC, LS had significantly more RWC as compared to MS and SS. However, at severe water stress (15% FC) there were no significant differences between seedling categories. Reductions in RWC and leaf water potential due to water stress were also reported by Morgan (1984), Liu *et al*. (2004) and Merchant *et al*. (2007). Leaf area decreased with water stress. Generally, leaf area in LS was relatively less affected as compared to MS and SS. The reduction in leaf area was correlated with water stress. However, at 15% FC there were no significant differences between seedling categories. Larger stocks of seedlings were more capable of acquiring soil moisture especially when competing with other vegetation (Lamhamedi *et al*., 1996; Mohammed *et al*., 1998; Pue´rtolas *et al*., 2003; Villar-Salvador *et al*., 2004a). Several investigators have reported a decrease in leaf growth of tree species due to water stress e.g. *Eucalyptus globulus* (Metcalfe *et al*., 1990) and mahogany (Okali & Dodoo, 1973). Reduction of lea area as a result of water stress has been considered by Hennessey *et al*. (1985) and Hibbs *et al*. (1995) as a morphogenetic adaptation to drought conditions. In the present study, biomass allocation was partitioned more towards the root system. This was indicated by the increase in root length and fresh and dry weight of the roots, whereas shoot length and fresh and dry weight of the shoot decreased with water stress. Similarly, root biomass increased by three folds in *Acacia tortilis* seedlings under water stress, however seedlings of *A. xanthophloea* showed no significant difference in R: S ratio between control and water stressed plants (Otieno *et al*., 2005). Tolerance of plants to water stress depends on their ability to biomass partitioning (Enquist & Niklas, 2002; Poorter *et al*., 2012). Biomass partitioning towards the roots increased with plant size. It is evident that under stress conditions more biomass was allocated towards the roots because they acquire resources necessary for growth as compared to stems which perform structural functions (Poorter & Nagel, 2000; Poorter *et al*., 2012; Tomlinson *et al*., 2013). Osorio *et al*. (1998); Ranney *et al*. (1990); and Rhodenbaugh & Pallardy (1993) reported that water stress affected biomass partitioning and growth of eucalypts. Water stress caused 100% mortality of small wheat plants and reduced growth and stomatal conductance of large plants (Olivas-Garcia *et al*. (2000); Panek & Goldstein (2001). Max survival of *Quercus petraea* seedlings under nursery conditions was recorded in seedlings from large (89%) and medium (91%) sized seeds (Tilki, 2010). Larger seedlings have greater root systems enabling them to tolerate water stress (Hines & Long, 1986; Luis *et al*., 2009). Seedlings usually allocate high biomass to develop the root system (Garkoti *et al*., 2003). Such adaptation is very critical especially in dry tropical forests with harsh periods of unpredictable droughts (Reich & Borchert, 1984; Ray & Brown, 1995; Burslem *et al*., 1996). If the root system is not well established after planting of seedlings in the field, they encounter water stress (Burdett, 1990; Grossnickle, 2000). Although increased biomass allocation to the roots is critical to acquire soil resources under drought conditions, however this was done at the expense of photosynthetic carbon (Ho *et al*., 2005). Consequently, this may reduce the overall plant growth (Nielsen *et al*. (2001). Nevertheless, Benincasa *et al*. (2013) reported controversial results as shoot/root ratio of *Brassica napus* increased in lab experiments and decreased in the greenhouse under salt stress. However, he attributed this controversy to time difference of stress application. Shoot size and shoot/root ratio are critical parameters especially in dry soil with high evaporation rate (Grossnickle, 2012).

Conclusions

Seedlings from large seeds grew better and more tolerant to water stress compared with seedlings from small seeds. The most important mechanism of *A. asak* seedlings to tolerate water stress was the increased root length and biomass partitioning towards the root system. There were significant differences between and within seedling size in their response to water stress. Thus, at the early restoration programs it would be more appropriate to rely on large sized seeds.

Acknowledgement

"The authors would like to extend their sincere appreciation to the Deanship of Scientific Research at King Saud University for its funding of this research through the Research Group Project No.RGP-VPP-226".

References

Axelson. E. and B. Axelson, 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. *Tree Physiol*., 2: 1898-204.

Benincasa, P., R..M. Pace, S. Quinet and M. Lutts. 2013. Effect of salinity and priming on seedling growth in rapeseed (*Brassica napus* var *oleifera* Del.). *Acta. Sci. Agron.,* 35(4): 479-486.

Buckley, R.C. 1982. Seed size and seedling establishment in tropical dune crest plants. *Biotropica,* 14: 314-315.

Burdett, A.N. 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. *Can. J. For. Res*., 20: 415-427.

Burslem, D.F., P.J. Grubb and I.M. Turner. 1996. Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica,* 28: 636-648.

Castro J, J.A. Ho´dar, J.M. Go´mez. 2006. Seed size. In: *Handbook of Seed Science and Technology,* (Ed.): A.S. Basra, Food Products Press/the Haworth Press, Inc., New York, pp. 397-427.

Clemensson-Lindell, A. and H. Persson. 1993. Long-term effects of liming on the fine-root standing crop of *Picea abies* and *Pinus sylvestris* in relation to chemical change in the soil. *Scand. J. For. Res*., 8: 384-394.

El Atta, H.A., I.M. Aref, A.S. Ahmed, P.R., Khan. 2012. Morphological and anatomical response of *Acacia ehrenbergiana* Hayne and *Acacia tortilis* (Forssk) Haynes subspp. *raddiana* seedlings to induced water stress. *Afr. J. Biotech*., 11(44): 10188-10199.

Enquist B.J. and K.J. Niklas. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Sci*., 295: 1517-1520.

Fenner, M. 1985. *Seed Ecology*. Chapman and Hall Ltd., London.

Foster, S.A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Bot. Rev*., 52: 260-299.

Garkoti, S.C., D.B. Zobel and S.P. Singh. 2003. Variation in drought response of sal (Shorea robusta) seedlings. *Tree Physiol.,* 23: 1021-1030.

Grossnickle, S.C. 2000 *Ecophysiology of northern spruce species: the performance of planted seedlings*. NRC Research Press, Ottawa.

Grossnickle, S.C. 2012. Why seedlings survive: influence of plant attributes. *New For*., 43: 711-738.

Hammond, D.S. and V.K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal and soil type in wet neotropical forests. *Ecol*., 76: 2544-2561.

Hennessey, T.C., L.K. Bair and R.W. McNew. 1985. Variation in response among three Alnus spp. clones to progressive water stress. *Plant and Soil*., 87: 135-141.

Hibbs, D.E., S.S. Chan, M. Castellano and C. Niu. 1995. Response of red alder seedlings to CO2 enrichment and water stress. *New Phytol*., 129: 596-577.

Hines, F.D. and J.N. Long. 1986. First-and second-year survival of containerized Engelmann spruce in relation to initial seedling size. *Can. J. For. Res.,* 16: 668-670.

Ho, M.D., J.C. Rosas, K.M. Brown and J.P. Lynch. 2005. Root architectural tradeoffs for water and phosphorus acquisition. *Func. Plant Biol.,* 32: 737-748.

Iortsuun, D.N., A.M. Chia and A.F. Adeola. 2008. The effect of seed mass and cotyledon removal on the germination and growth of fluted pumpkin (*Telfaria occidentalis* Hook. F). *Sci. World J*., 3(1): 25-31.

Khan, M.L. 2004. Effects of seed mass on seedling success in *Artocarpus heterophyllus* L., a tropical tree species of north-east India. *Acta Oecologica,* 25: 103-110.

Khera, N., A.K. Saxena and R.P. Singh. 2004. Seed size variability and its influence on germination and seedling growth of five multipurpose tree species. *Seed Sci. Technol.,* 32: 319-330.

Khurana, E. and J.S. Singh. 2000. Influence of Seed Size on Seedling Growth of Albizia procera Under Different Soil Water Levels. *Annal. Bot*., 86: 1185-1192.

Lamhamedi, M.S., P.Y. Bernier and C. Hebert. 1996. Effect of shoot size on the gas exchange and growth of containerized Picea mariana seedling under different watering regimes. *New For.,* 13: 207-221.

Linder, S. and B. Axelson. 1982. *Changes in carbon uptake and allocation patterns as a result of irrigation and fertilization in a young Pinus sylvestris stand.* In: *Carbon Uptake and Allocation in Subalpine Ecosystems as a Key* to Management. (Ed.): R H Waring. Oregon State University, Corvallis, Oregon. pp. 38-44.

Liu, L.X., X. Shou-Min and K.C. Woo. 2004. Watering regime effects on photosynthsis and the xanthophyll cycle in the tropical tree species *Acacia auriculiformis* in North Australi, N. Zealand J. Bot., 42: 949-957.

Lloret, F.C., C. Casanovas and J. Pen˜uelas. 1999. Seedling survival of Mediterranean shrubland species in relation to root: shoot ration, seed size and water and nitrogen use. *Func. Ecol.,* 199(13): 210-216.

Luis, V.C., J. Pue´rtolas, J. Climent, J. Peters, A.M. Gonza´lez-Rodrı´guez, D. Morales and M.S. Jimene´z. 2009. Nursery fertilization enhances survival and physiological status in Canary Island pine (*Pinus canariensis*) seedlings planted in a semiarid environment. *Eur. J. For. Res.,* 128: 221-229.

Martı´nez-Garza, C., V. Pen˜a, M. Ricker, A. Campos and H.F. Howe. 2005. Restoring tropical biodiversity: leaf traits predict growth and survival of latesuccessional trees in early-successional environments. *For. Ecol. Manage*., 217: 365-379.

Matyssek, R., G. Wieser, R. Ceulemans, H. Rennenberg, H. Pretzsch and K. Haberer. 2010. Enhanced ozone strongly reduces carbon sink strength of adult beech (*Fagus sylvatica*) - resume from the free-air fumigation study at Kranzberg *For. Environ Poll*., 158(8): 2527-2532.

Merchant, A., A. Callister, S. Arndt, M. Tausz and M. Adams. 2007. Contrasting physiological responses of six Eucalyptus species to water deficit. *Ann. Bot*., 100: 1-9.

Metcalfe, J.C., W.J. Davies and J.S. Pereira. 1990. Leaf growth of Eucalyptus globulus seedlings under water deficit. *Tree Physiol.,* 6: 221-227.

Mohammed, G.H., T.L. Noland and R.G. Wagner. 1998. Physiological perturbation in jack pine (Pinus banksiana Lamb.) in the presence of competing herbaceous vegetation. *For. Ecol. Manage*., 103(1): 77-85.

Moleele, M., M.S. Reed, L. Motoma and O. Seabe. 2005. Seed weight patterns of Acacia tortilis from seven seed provenances across Botswana. *Afr. J. Ecol*., 43:146-149.

Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.,* 35: 299-319.

Murphy, P.G. and A.E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica,* 18: 89-96.

Nielsen, K.L., A. Eshel and J.P. Lynch. 2001. The effect of phosphorus availability on the carbon economy of contrasting common bean (Phaseolus vulgaris L.) genotypes. *J. Expt. Bot*., 52: 329-339.

Nikolova, P.S., C.H. Zang and H. Pretzsch. 2011. Combining tree-ring analysis on stems and coarse roots to study the growth of forest trees: A case study on Norway spruce (Picea abies [L.] H. Karst). *Tree Struct. Func*., 25(5): 859-872.

Okali, D.U.U. and G. Dodoo. 1973. Seedling growth and transpiration of two West African mahogany species in relation to water stress in the root medium. *J. Ecol*., 61: 421-438.

Olivas-Garcia, J.M., B.M. Cregg and T.C. Hennessey. 2000. Genotypic variation in carbon isotope discrimination and gas exchange of ponderosa pine seedlings under two levels of water stress. *Can. J. For. Res*., 30(10): 1581-1590.

Osorio, J., M.L. Osorio, M.M. Chaves and J.S. Pereira. 1998. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in Eucalyptus globulus. *Tree Physiol.,* 18: 363-373.

Otieno, D.O., M.W.T. Schmidt, S. Adiku and J. Tenhunen. 2005. Physiological and morphological responses to water stress in two *Acacia* species from contrasting habitats. *Tree Physiol*., 25: 361-371.

Ovcharov, K.E. 1977. *Physiological Basis of Seed Germination*. Amerind Publ. Co. Pvt. Ltd. New Delhi.

Panek, J.A. and A.H. Goldstein. 2001. Response of stomatal conductance to drought in ponderosa pine: implications for carbon and ozone uptake. *Tree Physiol*., 21(5): 337-344.

Pang, J., J. Yang, H.M. Kadambo, M. Siddique, H. Lambers, M. Tibbett and A. Ryan. 2011. Contrasting responses to drought stress in herbaceous perennial legumes. *Plant Soil.,* 348: 299-314.

Paz, H. and M. Martinez-Ramos. 2003. Seed mass and seedling performance within eight species of Psychotria (Rubiaceae). *Ecol*., 84: 439-450.

Pinto, J.R., J.D. Marshall, P.K. Dumroese, A.S. Davis and D.R. Cobos. 2012. Photosynthetic response, carbon isotopic composition, survival, and growth of three stock types under water stress enhanced by vegetative competition. *Can. J. For. Res*., 42: 333-344.

Poorter, H. and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO2: nutrients and water: a quantitative review. *Aust. J. Plant Physiol*., 27: 595-607.

Poorter, H., K.J. Niklas, P.B. Reich, J. Oleksyn, P. Poot and L. Mommer. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.,* 193: 30-50.

Pretzsch, H. and J. Dieler. 2010. The dependency of the size growth relationship of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in forest stands on long-term site conditions, drought events, and ozone stress. *Trees,* 25(3): 255-369.

Pue´rtolas, J., L. Gil and J.A. Pardos. 2003. Effects of nutritional status and seedling size on field performance of Pinus halepensis planted in former arable land in the Mediterranean basin. *For*., 76: 159-168.

Ranney, T.G., T. Whitlow and N.L. Bassuk. 1990. Response of five temperate deciduous tree species to water stress. *Tree Physiol*., 6: 439-498.

Ray, G.J. and B. Brown. 1995. Restoring Caribbean dry forests: evaluation of tree propagation techniques. *Rest. Ecol*., 3: 86-94.

Reich, P.B. and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J. Ecol*., 72: 61-74.

Rhodenbaugh, E.J. and S.G. Pallardy. 1993. Water stress, photosynthesis and early growth patterns of cuttings of tree Populus clones. *Tree Physiol*., 13: 213-226.

Sa´nchez-Vela´squez, L.R., S. Quintero-Gradilla, F. Arago´n-Cruz and M.R. Pineda-Lo´pez. 2004. Nurses for Brosinum alicastrum reintroduction in secondary tropical dry forest. *For. Ecol. Manage*., 198: 401-404.

SAS (1997). *SAS institute INC*., Cary, North Carolina.

Tilki, F. 2010. Influence of acorn size and storage duration on moisture content. *J. Environ. Biol*., 31: 325-328.

Tomlinson, K.W., F. Langevelde, D. Ward, F. Bongers, D.A. Silva, H.H, Prins, S. Bie and F.J. Sterck. 2013. Deciduous and evergreen trees differ in juvenile biomass allometries because of differences in allocation to root storage. *Ann. Bot*., 112: 575-587.

Villar-Salvador, P., R. Penuelles, E. Enriquez, J. Penuelas and J.L. Rubira. 2004a. Nursery cultivation regimes, plant functional attributes, and field performance relationship in Mediterranean oak Quercus ilex L. *For. Ecol. Manage*., 196: 257-266.

Walters, M.B. and P.B. Reich. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecol*., 81: 1887-1901.

Yanlong, H.E., W. Mantang, W. Shujun, Z. Yanhui, M. Tao and D. Guozhen. 2007. Seed size effect on seedling growth under different light conditions in the clonal herb *Ligularia virgaurea* in Qinghai-Tibet Plateau. *Acta. Ecol. Sinn*., 27(8): 3091-3108.

(Received for publication 24 February 2015)