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Effect of Hormonal Seed Priming on Germination, Growth, Yield and Biomass Allocation in Soybean Grown under Induced Drought Stress

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ABSTRACT

Seed priming has potential to improve seedling development and plant growth under environmental stress. In this study, seeds of soybean cultivar LS678 and TGx1835-10E were pretreated with an optimum level of benzyladenine (4.87 mgL^{-1}) before sowing into pots containing pasteurised mixture of vermiculite and sand. Plants were grown up to V3 stage before exposure to moderate and severe drought stress. According to the results, germination was rapid in hydroprimed seeds than BA primed seeds, which took longer to emerge. However, growth, yield and biomass of BA primed plants were increased (number of branches per plant- 7.32, flowering-87.6%, 100 seed weight- 22.6 g, overall biomass fraction- >40.5%) compared to plants developed from hydroprimed seeds (number of branches- 3.61, seed weight- 19.2 g, biomass- <12%) under similar growth conditions. This study indicated that, hormonal seed priming with BA reasonably enhanced soybean growth, particularly root biomass, flowering and fruiting. These effects further suggest that BA may play a significant role in improving drought tolerance in soybean.

Key words: Benzyladenine, Biomass, Drought, Priming, Soybean.

INTRODUCTION

The vulnerability of soybeans to adverse environmental conditions negatively influence their growth and productivity in many countries. In South Africa, like rest of the countries in the sub-Saharan region, soybean cultivation is negatively affected by prolonged water shortage, resulting in drought stress (Ortiz, 1998). Drought is one of the most important abiotic stresses that drastically reduce agricultural productivity of many crops, especially by negatively altering crucial plant physiological and biochemical processes (Jewell *et al*., 2010; Wei *et al*., 2018; Rangwala *et al*., 2018). Wei *et al.* (2018) further indicated that drought's severity in crops varies according to growth stages, with greatest losses during flowering-fruiting stage and pod filling. This problem can be resolved by a full use and adoption of novel physiological or biotechnological approaches that function to improve soybean growth under different environmental stress conditions, particularly those that improve crop tolerance to abiotic stress. Amongst the approaches, as reviewed by Jewell *et al.* (2010), genetic/physiological mechanisms targeted for manipulation of soybean growth to advance drought or chilling stress resistance could be recommended. Such techniques include the use of plant growth regulators such as; abscisic acid (ABA) and the most potent synthetic cytokinin compound; 6-benzylaminopurine or benzyladenine (BA) that regulates adaptive responses to environmental stresses in plants (Liu *et al*., 2000; McCourt and Creelman, 2008; Sardoei, 2014; Atteya *et al*., 2018). Plant hormones like ABA have been implicated in a variety of physiological processes triggered by stress, ranging from dormancy of seeds to chlorophyll biosynthesis (McCourt and Creelman, 2008). Meanwhile, cytokinins like BA are best known for promoting cell proliferation, delaying tissue senescence, inhibiting root formation and enhancing chloroplast development (Mangena *et al*., 2015). However, the effect of BA on growth of important agroeconomic crops like barley, soybean and wheat have been rarely investigated. This hormones remain the most predominantly used cytokinin in *in vitro* plant tissue culture and *in vivo* agricultural applications to stimulate and synchronise plant processes such as flowering, fruiting and biomass allocations (Mansour *et al*., 2014). This hormone has been widely reported to significantly increase fresh and dry biomass fractions of leaves, roots and stems in many plant species including rice, spurges and soybean (Saadawy and Abdel-Moniem, 2015; Mangena *et al*., 2015; El-Ghamery and Mousa, 2017). Notwithstanding the larger number of reports on the effect of cytokinin application on the growth and *in vitro* regeneration of legumes, the effects of these hormones on the biomass, growth and yield of soybean have

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not been well documented. Therefore, the objective of this study was to investigate the effect of benzyladenine (BA) on plant biomass allocation, growth and yields of soybean under moderate and severe drought stress.

MATERIALS AND METHODS

This research was conducted at Turfloop, University of Limpopo, Republic of South Africa, in September 2017 to March 2018. Freshly harvested soybean [*Glycine max* (L) Merrill] seeds, comprising of two commonly cultivated cultivars; TGx1835-10E and LS678 were used. These two cultivars had determinate growth habit, widely adapted to and recommended for the cultivation of soybean in South Africa. According to Grain South Africa (GRAIN SA) and International Institute of Tropical Agriculture (IITA), the soybeans were considered susceptible and less tolerant to drought stress. Seeds were surface sterilised overnight for 16-hours using chlorine gas (Mangena and Mokwala, 2019). The disinfected seeds were then imbibed overnight in a priming solution containing sterile deionized water and 4.87 mgL^{-1} BA. Seeds imbibition was done in the dark (24±2°C), with gentle agitation on a Labcon platform shaker (speed of 175 rpm) at room temperature. The BA concentration chosen for this experiment was based on findings of previous studies. The imbibed seeds were sown on pasteurised mixture of vermiculite and sand at ratio 2:1. The vermiculite and sand were specifically used as a support medium, because they contained small amount of thin, flat silt and provide a nutrient-free medium. This mixture was in pure state, had high water retention time and little or no impurities. Soybean seeds soaked in water (hydropriming) were treated as a negative control. Meanwhile, soybean plants developed from BA-primed seeds were used as a positive control and as experimental treatment. Seed germination was conducted with 30 replications of two seeds per pot, placed under controlled conditions.

In order to examine the effects of BA priming on seed germination, germination was recorded on a daily basis as seedling emergence. The final germination percentage (G_f%) was calculated using the equation below where; n_f and N were the final number of seeds germinated and total number of seeds tested, respectively. Following germination and seedling development, BA-primed and hydroprimed soybean plantlets were still kept under the same growth conditions before being transferred to a glasshouse for moderate and severe drought stress evaluations. All plantlets were kept in a growth room with light maintained between 160 and 200 µmol m^{-2}s^{-1} as well as 60-70% humidity for 3-4 weeks.

$$G_f\% = \left(\frac{n_f}{N}\right) \times 100$$

Drought stress treatment

All plants were irrigated daily with distilled water and once a week with half-strength Hoagland solution to ensure better seedling and plant establishment until they reached V3 growth stage identified as an appropriate stage to induce drought stress in soybean (Dong *et al*., 2019). After this stage, soybean plants, with only one plant per pot, were randomly subdivided into groups consisting of 30 replicates each. First group was used as a negative control with water deficiency, second group was used as experimental BA-primed plants subjected to moderate and severe drought stress and third group was well-watered BA-primed plants used as positive control. The sub-samples were then further separated into 15 pot plants, for vegetative growth and yields analyses. Plants were then transferred to a glasshouse under natural conditions and water deficit stress was then imposed on them. The two irrigation regimes were conducted by withholding water, where well-watered soybean plants served as a positive control. Water stress was imposed by watering the plants to saturation once in 6-days for moderate stress and once in 9-days for severe stress until they reached late V5 stage when blooming starts for plants used for biomass analysis and at R7 stage for yield analysis (Mangena, 2018). In order to evaluate drought-related characteristics, parameters including plant biomass (for leaves, stems and roots), mean number of branches, flowering and fruit set were analysed. The biomass allocation ratios (*BR*) were calculated according to the equation below, which were measured under drought stress and controls; where *Dw* is dry weight of plant organ (root/stem/leaf) and *Tw* is total dry weight of the plant in g g^{-1} (Pooter *et al*., 2011).

$$BR = \frac{Dw}{Tw}$$

The biomass fractions (*BF*) with percentage for each plant organ (root/stem/leaf) were calculated using the formula below, where *Fw* refers to fresh weight of each plant organ and *Dw* is the dry weight.

$$BF = \frac{Fw - Dw}{Fw} \times 100$$

Growth conditions and data analysis

A growth room used for germination and seedling development was equipped with white fluorescence light at 160-200 µmol m^{-2}s^{-1} using PHILIPS TL-D 58W/33-6407D bulbs, at 25±2°C temperature and 16-hour photoperiod. The experiment contained 30 replicates each and repeated three times. Data of experiment was subjected to variation analysis, where all data were statistically analysed using two-way analysis of variance (ANOVA) at 0.05 confidence level.

RESULTS AND DISCUSSION

Effect of Priming on Germination and Seedling Growth

This study investigated the effects of hormonal priming on soybean germination, growth, yield and biomass allocation under moderate and severe drought stress. According to the results, the performance of the two cultivars were significantly influenced by priming of seeds in a solution containing BA. There were significant differences in germination between hormone primed and hydroprimed seeds. Priming of seeds significantly affected overall percentage germination with 86.5 and 85.5% recorded in LS678 and TGx1835-10E, meanwhile 95.0 and 94.0% were obtained for the same cultivars using hydroprimed seeds, respectively (Table 1). In distinction, hydroprimed seed germination was rapid and developed seedlings exhibited thin elongated hypocotyls, elongated epicotyls and long primary roots with lateral roots.

These observations were similar to previously reported findings in the germination of *Nigella sativa* L. and *Allium cepa* L. seeds which were reported to be influenced by BA (Zhao *et al*., 1992). In soybean, it was also indicated that, pretreatment of seeds with BA caused a reduction in germination speed, epicotyl growths and primary as well as lateral root formation, especially when applied in amounts higher than 4.87 mgL^{-1} of BA used (Mangena and Mokwala, 2018). The role of BA in changing seedling morphological characteristics such as; swollen underdeveloped radicles, thicker hypocotyls and stunted shoots was fully accounted for (Mangena *et al*., 2015; Sale, 2016; Suo *et al*., 2017). In line with this study, it was also reported that, germination can be raised by soaking seeds in a solution containing a similar amount of BA, although its effects could be inhibitory and it was better used alone than in combination with any other hormone, for example GA_3 (Gao *et al*., 2015).

Table 1: The germination of hydroprimed and BA-primed (4.87 mgL^{-1}) soybean seeds, cultivar TGx1835-10E and LS678.

	Germination (%) ± SE
BA-primed with moderate stress	
TGx1835-10E	85.5 ± 0.176^a
LS678	86.5 ± 0.146^b
BA-primed with severe stress	
TGx1835-10E	85.5 ± 0.176a
LS678	86.5 ± 0.146^b
BA-primed without water stress	
TGx1835-10E	85.5 ± 0.176^b
LS678	86.5 ± 0.146^a
Hydroprimed with moderate stress	
TGx1835-10E	94.0 ± 0.041^b
LS678	95.0 ± 0.021^a
Hydroprimed with severe stress	
TGx1835-10E	94.0 ± 0.041^b
LS678	95.0 ± 0.021^a

Mean values accompanied by different superscript letters are statistically different at p-value less than 0.05. SE refers to standard error.

Influence of priming on growth and yield

The present results also showed that different growth and yield characteristics were recorded from plants derived from hormone primed and hydroprimed soybean seeds. The highest vegetative growth ratio was obtained in plants used as a positive control, BA primed plants subjected to moderate stress followed by plants that experienced severe water deficit stress. Plants developed from hydroprimed seeds had a poor growth response amongst all plants subjected to drought stress. As expected, BA primed positive control with normal irrigation had the highest mean number of branches (5.22, 7.32) flowering (83.6, 87.6) and mean number of pods (36.4, 52.7) achieved per plant for TGx1835-10E and LS678, respectively (Table 2). Water stressed plants developed from BA primed seeds also recorded a significantly high number of branches per plant (4.32, 6.61), flowering (22.4, 41.6), pods (11.4, 39.5) than hydroprimed plants which mostly recorded between 0.0 to the highest of 19.6% in all parameters evaluated (Table 2). For yield analysis, roughly 8 out of 15 moderately stressed BA-primed plants and 4 out of 15 severely stressed BA-primed plants formed premature flower buds, which reached anthesis. However, the results

Table 2: Vegetative growth and yield responses of soybean plants developed from BA-primed and hydroprimed seeds.

	Mean no. of branches/plant	Flowering (%)	Mean no. of pods/plant	Mean seed no./pod	100 seed weight (g)	Sig. (p-value < 0.05)
BA-primed with moderate stress						
TGx1835-10E	4.32^d	37.5^a	27.2^b	3.0	21.7^a	0.028
LS678	6.61^a	41.6^b	39.5^a	3.0	20.3^b	0.102
BA-primed with severe stress						
TGx1835-10E	4.47^c	22.4^d	13.6^c	3.0	19.8^b	0.053
LS678	5.67^b	35.6^c	11.4^d	3.0	20.6^a	0.011
BA-primed without stress						
TGx1835-10E	5.22^c	83.6^b	36.4^c	3.0^a	22.6^a	0.131
LS678	7.32^a	87.6^a	52.7^a	3.0^a	22.2^a	0.022
Hydroprimed with moderate stress						
TGx1835-10E	4.47^d	19.4^d	5.0^c	3.0^a	17.8^c	0.053
LS678	5.61^b	12.6^c	15.0^d	3.0^a	19.2^a	0.011
Hydroprimed with severe stress						
TGx1835-10E	1.32^f	0.00^b	0.00^b	0.0	0.00^b	-
LS678	1.58^e	0.00^a	0.00^a	0.0	0.00^b	-

Values within columns followed by similar superscript letters are not significantly different at 0.05 p-value according to ANOVA.

clearly showed that lack of water affected anthesis by causing flower abortion and also affected yield by influencing seed filling as indicated by the mean pod number and low 100-seed weights recorded in Table 2. Furthermore, TGx1835-10E responded less effective than LS678 and recorded significantly lower values than the overall response of LS678. LS678 gave a variably high vegetative growth and yield response during moderate and severe water deficit stress than TGx1835-10E. But, all mean values were significantly lower than the responses of the same cultivars when used as a positive control (Table 2).

Additionally, across the board increases were observed in yield, determined by the highest number of flowers, number of pods and 100-seed weight in LS678 than TGx1835-10E. Although, TGx1835-10E recorded some few higher percentages in flowering and mean weight for 100 seeds weight than LS678 (Table 2). Therefore, soybean plants developed from seeds treated with BA showed better growth and reproductive traits (flowering and pod production) under drought stress than plants used as a negative control, which were harshly affected by similar drought conditions. Moreover, there were no flowers and pods produced by plants used as negative control without priming, a very poor response compared to all plants which had high percentage of flowering and fruit set (Table 2). Those better performing plants also had typically high 100-seed weights attributed to adequate water, BA hormone and availability of nutritional resources that were required during pod setting and seed filling.

Effect of Priming on Biomass Allocation

In concurrence with the vegetative growth responses indicated above, the overall highest biomass fraction was observed in plants used as positive control followed by BA-primed plants subjected to moderate and severe stress and the least was found on plants used as a negative control, respectively. Significant differences were observed on plant biomass fractions as shown in Fig 1 (a, b, c, e, f and g with BA priming) compared to hydroprimed plants (Fig 1 d and h) for both cultivars and their ratios as shown in Table 3. There was also a high variation between root biomass allocations compared to other biomass fractions of stems and leaves under drought stress. Generally, this was the case although, the highest biomasses of 68.158 and 66.567% were observed in stems and roots fractions of soybean LS678 positive controls (Fig 1 g). As a result, the leaf and stem biomass fractions of the experimental LS678 plants were drastically decreased by severe drought stress as indicated in Table 3 and Fig 1, with some tolerance being observed only in the roots. However, TGx1835-10E root biomass was higher than LS678 root fraction under moderate stress and even highest compared to the leaf fractions than stem biomass recorded under similar stress conditions. All BA treated plants were able to partly tolerate moderate drought stress, particularly, compared to plants used as negative control, which had the least root, stem and leaf biomass allocations. A biomass decrease below 12% was recorded in both LS678 and TGx1835-10E used as negative controls (Fig 1 d, h). Similar findings were made by Gao *et al*. (2015) and Sale (2016) in African locust bean using 20% BA diluted in 100 mL distilled water. Other negative effects, including a 10% decline in biomass fractions of roots, stems and leaves were attributed to severe water deficit with consequence effects on vegetative growth (Jewell *et al*., 2010; Kurnet *et al*., 2016). Similar effects were also highlighted when soybeans were subjected to drought stress during different stages of their growths without priming (Wei *et al*., 2018).

Therefore, all growth and yield effects could be attributed to seed priming with BA in addition to drought, because this hormone was also used to regulate growth of many plant species resulting in higher plant growth rates

Table 3: The biomass ratios of leaves, stems and roots measured after drought stress treatment at late V5 growth stage when blooming begin.

	Stem ratio (g g^{-1})	Leaf ratio (g g^{-1})	Root ratio (g g^{-1})	Sig. (p-value < 0.05)
BA-primed with moderate stress				
TGx1835-10E	1.78^{a}	1.35^{b}	1.26^{b}	0.011
LS678	1.74^{a}	1.05^{c}	1.22^{b}	0.027
BA-primed with severe stress				
TGx1835-10E	1.43^{b}	1.04^{c}	1.56^{a}	0.116
LS678	1.05^{c}	1.62^{a}	2.14^{c}	0.008
BA-primed without water stress				
TGx1835-10E	4.93^{b}	6.62^{a}	5.84^{b}	0.644
LS678	6.28^{a}	5.94^{b}	5.92^{a}	0.536
Hydroprimed with moderate stress				
TGx1835-10E	1.63^{d}	2.04^{d}	2.56^{d}	0.026
LS678	2.81^{c}	3.20^{c}	3.62^{c}	0.111
Hydroprimed with severe stress				
TGx1835-10E	1.35^{f}	0.52^{e}	1.84^{f}	0.198
LS678	1.44^{e}	1.62^{e}	1.99^{e}	0.017

Mean values accoanied by different superscript letters are statistically different at p-value less than 0.05. gg^{-1}, refers to gram per gram of biomass dry weight.

when it was used at 100-200 mgL^{-1} BA, with the involvement of GA_3 under pot cultivation conditions of *Ficus benjamina*, *Schefflera arboricola* and *Dizigotheeca elagantissima* plants (Mansour *et al*., 2014). In line with the findings in this study, other plant growth regulators like uniconazole were also reported to induce notable increases in the root biomass fractions than stem and leaf biomass allocations, which were rather reduced compared to their controls (Gao *et al*., 2015). However, findings made in this study and others (Mazrou *et al*., 1994; Mansour *et al*., 2014; Raveendra *et al*., 2014; Gao *et al*., 2015; Verma *et al*., 2016), especially on cytokinins and initiated root biomass are in contradiction with other findings that showed that cytokinins (at 0 to 200 mgL^{-1}) inhibit root and shoot growth under different *in vivo* growth conditions (Sardoei, 2014). As the causal relationship of the changes in seedling characteristics and subsequent variations in the growth, yield and biomass allocation observed in this study may still need to be further

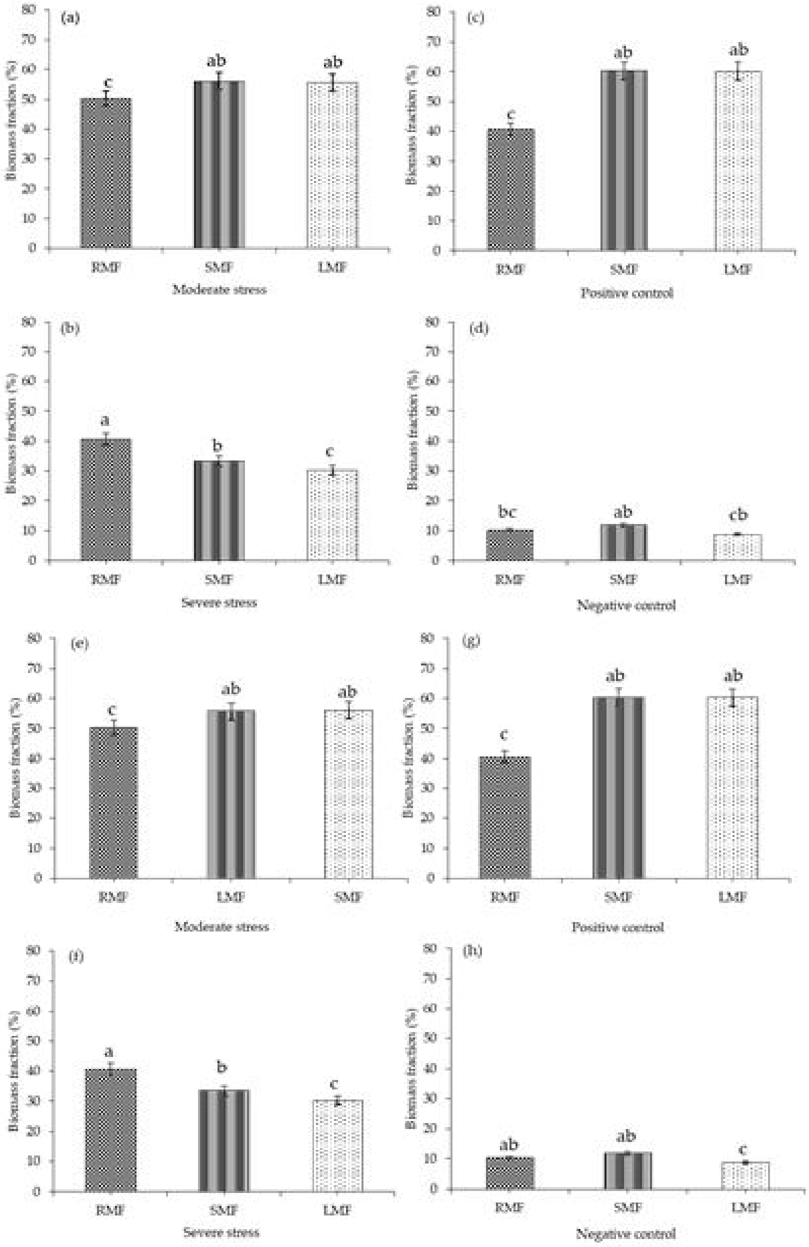

Fig 1: Comparison of total percentage biomass fractions in leaves, stems and roots of TGx1835-10E. (a- moderate drought stress; b- severe drought stress; c- BA-primed positive control with normal irrigation and d- hydroprimed negative control plants) and LS678 (e- moderate drought stress; f- severe drought stress; g- BA-primed positive control with normal irrigation and h- hydroprimed negative control plants) soybean plants pretreated with 4.87 mgL^{-1} BA under different water stress. RMF: Root Mass Fraction. SMF: Stem Mass Fraction. LMF: Leaf Mass Fraction. Percentage biomasses with similar letters above percentile bars did not differ when compared at 5% probability level using ANOVA.

investigated. Particularly, to involve factors such as the genotype, seed viability and the biochemical effects of BA seed pretreatment under drought stress conditions. These findings clearly demonstrated the importance of BA on obliviating poor growth effects under environmental stress as reported in the cultivation and productivity of other recalcitrant crops (Boschi *et al*., 2016; Suo *et al*., 2017).

CONCLUSION

The role of BA in promoting shoot growth has been long known, but its involvement on overall growth, yields and biomass allocations in soybean was unclear. Therefore, this study has provided more insights on the use of BA in improving these plant growth parameters, particularly its influence on root biomass than stem and leaf biomass fractions under moderate and severe drought stress. These effects further suggests that BA may play a significant role in conferring drought tolerance in the two soybean cultivars used.

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