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*Full Length Research Paper*

# Physiology and productivity of rice crop influenced by drought stress induced at different developmental stages

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**Rice is sensitive to moisture stress and in view of the water scarcity in the coming years, it is imperative to evaluate the performance of rice cultivar under moisture deficit. The present study aimed to evaluate the physiological responses of two rice cultivars under drought stress induced at panicle initiation and soft dough stages. The seeds of BAS-385 and KS-282 were soaked in ABA ($10^{-6}$ M) prior to sowing. Foliar application of ABA ($10^{-6}$ M) was made at tillering stage, 40 days after sowing (40 DAS) in both cultivars. Drought stress was induced at panicle initiation (PI) (65 DAS) and soft dough (SD) (105 DAS) stages with re-watering at incipient wilting (12% soil moisture). Drought induced significant decrease in endogenous level of IAA, GA, sugar and protein contents in leaves at SD stage, while ABA and proline contents increased significantly as compared to control. In grains, drought induced decreases in IAA, sugar and protein content were greater at PI stage in both cultivars. Stomatal resistance was significantly increased in flag and penultimate leaves at PI stage. ABA treatments ameliorated the adverse effects of drought stress for most of the physiological parameters but were ineffective to restore the drought-induced decrease in GA content. On-rewatering, the recovery of prestressed plants was significantly enhanced under ABA seed soaking and foliar spray treatments as compared to drought alone. It is inferred that the mechanism of ABA-induced tolerance to drought stress appears to be involved in maintenance of water budget by decreasing GA, increasing stomatal resistance and by osmoregulation as observed by increase in proline accumulation, and enhanced grain filling to bring early maturity in rice over control.**

**Key words:** Drought stress, rice cultivars, panicle initiation, soft dough.

## INTRODUCTION

Among the known abiotic stresses, drought is the most damaging one that affects today's agriculture. It is a multidimensional stress affecting plants at various levels of their organization (Blum, 1996). At the whole plant and crop levels, the plant response to drought is complex because it reflects the integration of stress effects and responses at all underlying levels of organization over space and time. The effect of stress is usually perceived as a decrease in photosynthesis and growth (Cornic and Massacci, 1996; Mwanamwenge et al., 1999).

Phytohormones are known to play crucial role in plant growth and development (Beaudoin et al., 2000; Hansen and Grossmann, 2000) in response to environmental stress. ABA is one of the stress hormones that plays a critical role in regulating plant water status and osmotic stress tolerance (Luan, 2002; Zhu, 2002; Ramachandra et

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**Abbreviations: DAS,** Days after sowing; **PI,** panicle initiation; **SD,** soft dough; **IAA,** indole acetic acid; **GA,** gibberellic acid; **ABA,** abscisic acid.

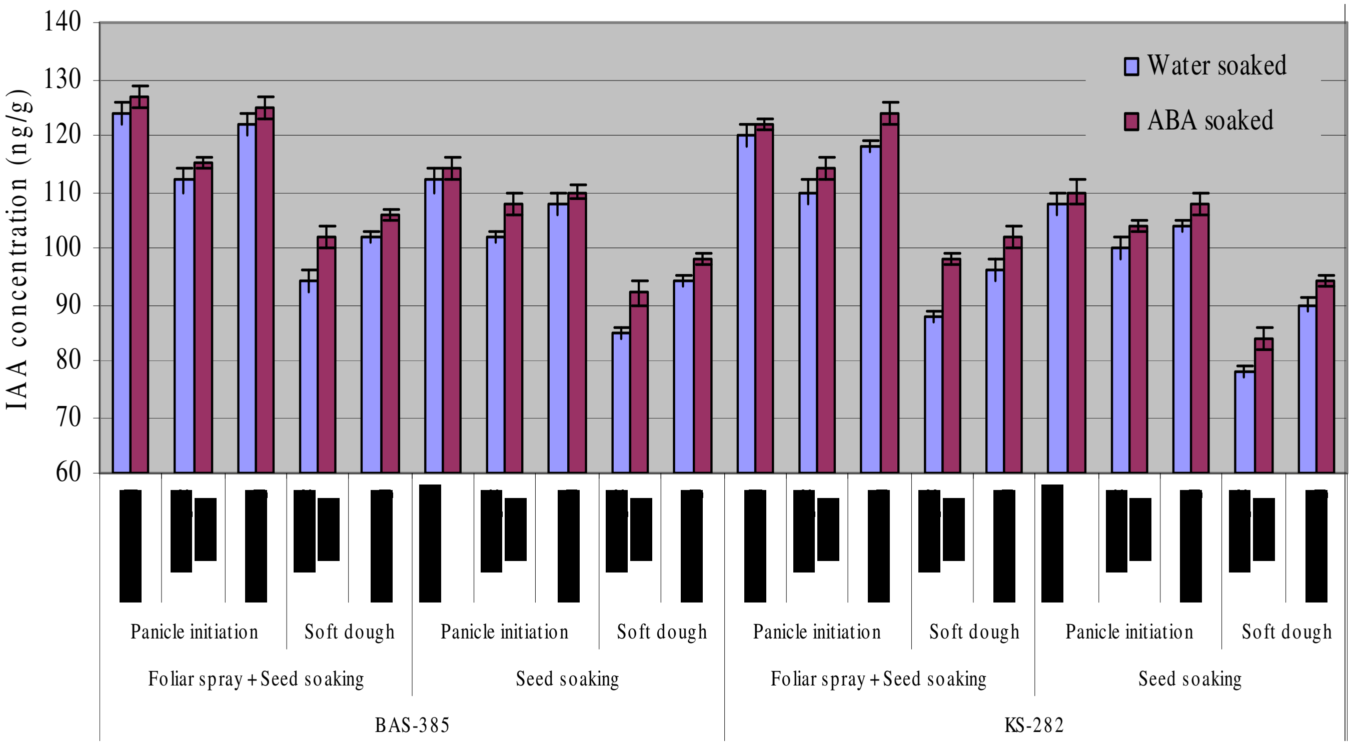


**Figure 1.** Effect of drought stress on IAA content (ng/g) in leaves of cv. BAS-385 and KS-282.

al., 2004; Bonetta and Mccourt, 1998; Mahajan and Tuteja, 2005) as well as various aspects of growth by regulating dormancy, maturation and adaptation to abiotic stresses (Beaudoin et al., 2000., Zhang et al, 2006). ABA can act as a long distance communication signal between water deficit roots and leaves by inducing the closure of stomata and reducing water loss through transpiration (Morgan, 1990; Davies and Zhang, 1991) and might promote grain filling through regulating the sink's strength (Yang et al., 1999). So, the present study was conducted to understand the physiology of drought tolerance with particular emphasis on the role of ABA under induced moisture stress levels at the panicle initiation (PI) and soft dough stages in rice crops.

## MATERIALS AND METHODS

A pot experiment was conducted in triplicate at National Agricultural Research Center (NARC) Islamabad, Pakistan. Seedlings of two indigenous rice cultivars cv. BAS-385 and KS-282, raised from their seeds soaked in water and ABA ($10^{-6}$ M) for 8 h prior to sowing, were planted in pots (27 x 27 inches) filled with soil and farmyard manure in the ratio 1:6. Fertilizer was applied in the form of di-ammonium phosphate (DAP) and Urea (125 g/pot). Foliar application of ABA ($10^{-6}$ M) was made at tillering stage 40 days after sowing (DAS). The plants were subjected to drought stress at panicle initiation (65 DAS) and soft dough (105 DAS) stages. Moisture (30%) was retained in half of drought stressed plants. Re-watering was done at incipient wilting at 12% soil moisture contents. The rice samples were collected at soft dough and mature grain stages for the analysis of biochemical parameters viz., sugar contents (Dubo et al., 1956; Johnson et al., 1966), protein contents (Lowry et al., 1951) and proline contents (Bates et al., 1973). Stomatal resistance (s.cm$^{-1}$) was measured using diffusion porometer (Delta T Devices, U.K) following the method of Moneith et al. (1988) at panicle initiation and soft sough stages. Extraction and purification of IAA and GA was made according to Kettner and Doerffling (1995), whereas for ABA it was done by following Hansen and Doerffling (1999). The wavelength used for the detection of IAA was 280 nm (Sarwar et al., 1992), whereas for GA (Li et al., 1994) and ABA (Hansen and Doerffling, 1999) analysis, it was adjusted at 254 nm. Data were analyzed statistically by analysis of variance (completely randomized factorial design) and treatment means were compared using Duncan's multiple range test (DMRT) using MSTAT-C version 1.4.2 (Freed and Eisensmith, 1991).

## RESULTS AND DISCUSSION

### Endogenous level of phytohormones

ABA foliar spray and ABA foliar spray + seed soaking treatments has markedly increased IAA production under unstressed conditions both in leaves and grains in both cultivars at panicle as well as soft dough stages as compared to control (Figures 1 and 2). This may be due to promotery and inhibitory effects of endogenous and exogenous plant growth substances on plant growth and development.

Drought stress decreased IAA contents in leaves at panicle initiation and soft dough stages under seed soaking and seed soaking + foliar spray treatments but its

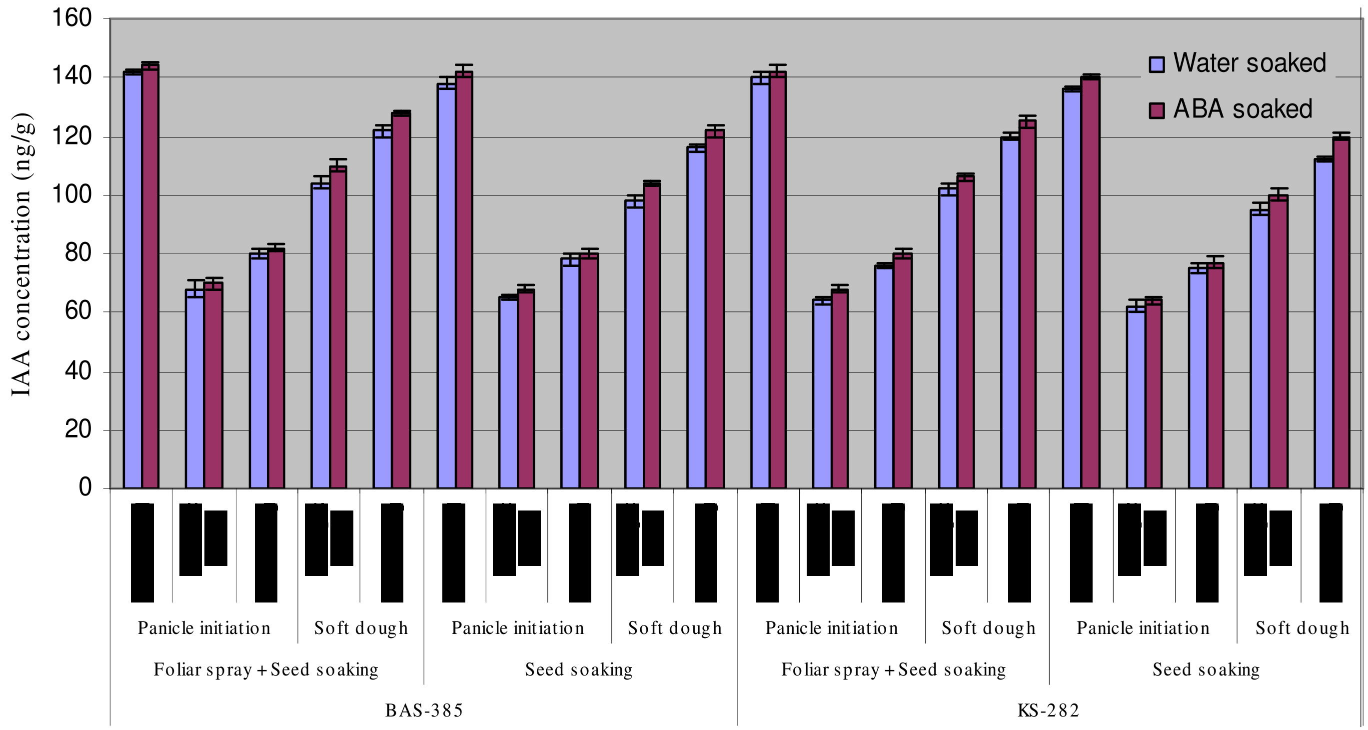


**Figure 2.** Effect of drought stress on IAA content (ng/g) in grains of cv. BAS-385 and KS-282.

magnitude of reduction was more significant at soft dough stage while, in grains the IAA concentration decreased significantly in both seed soaking alone as well as seed soaking in combination with foliar spray treatments, but the reduction was more effective in seed soaking treatment at panicle initiation stage in both cultivars (Figures 1 and 2). The ABA increased endogenous concen-tration of IAA over that of drought alone. This may be due to the role of ABA in plant growth and development under the stressed environment. The observed effect of drought in leaves at panicle initiation stage may be attributed to greater induction of metabolic activity of the vegetative parts at panicle initiation as compared to soft dough stage which might enable plants to sustain adverse effects of water deficit. One of the mechanisms of ABA induced tolerance to moisture stress might be the change in the ratio of growth promoting to growth inhibi-ting hormones and IAA is one of them. It had also been reported that ABA enhanced the growth of maize plant under water deficit conditions (Spollen et al., 2000; Mahajan and Tuteja, 2005). Plant responses to stress can also be determined by the variations in IAA and ABA levels (Naqvi, 1999).

The IAA content of grain was higher than leaf IAA at all stages and in all treatments of both varieties. The difference in response to drought for leaf and grain IAA was greater susceptibility of grains to drought both in the control and ABA treated plants accompanied by slow rate of recovery on rewatering. ABA seed soaking + foliar spray treatments and ABA foliar spray alone provided a better recovery than that of drought alone. Changes in hormonal concentration might occur upon rewatering, which in turn enhanced growth and development in plants (Yang et al., 2001). A rapid decrease in leaf ABA concentration to the concentration observed in unstressed plants and an increase in its metabolite phasic acid has been reported to occur after rehydration (Lian and Zhang, 1999; Alves and Setter, 2000; Zeevaart, 1980).

The effect of drought in grains was less at soft dough than that of panicle initiation stage. Seed soaking treatment had relatively less decrease in IAA content due to drought as compared to seed soaking + foliar spray in both the varieties.

The ABA foliar spray and ABA foliar spray + seed soaking treatments have markedly increased GA concentration under unstressed conditions both in leaves and grains (Figure 3 and 4). It may be possible that better root proliferation is caused by ABA treatments and the roots tips are the sites for GA synthesis. ABA is involved in the formation of root hairs and lateral roots (Hose et al., 2002). Large quantities of GA are produced by the roots of plants (Oda et al., 2003). Drought stress decreased GA content in leaves as well as in grains at panicle initiation and soft dough stage but decrease was significant at soft dough stage under both seed soaking as well as seed soaking + foliar spray treatment in both cultivars (Figures 3 and 4).

GA content was much higher than IAA content both in leaves and spikes of both cultivars in all treatments including ABA seed soaking as well as ABA seed soaking

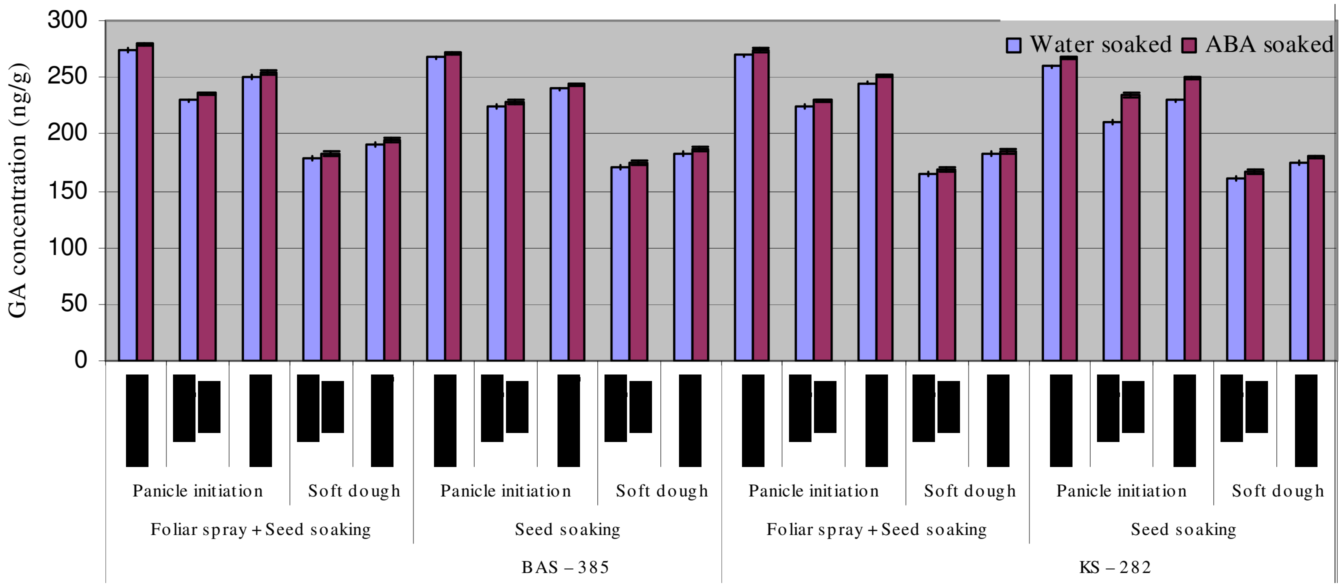


**Figure 3.** Effect of drought stress on GA content (ng/g) in leaves of cv. BAS-385 and KS-282.

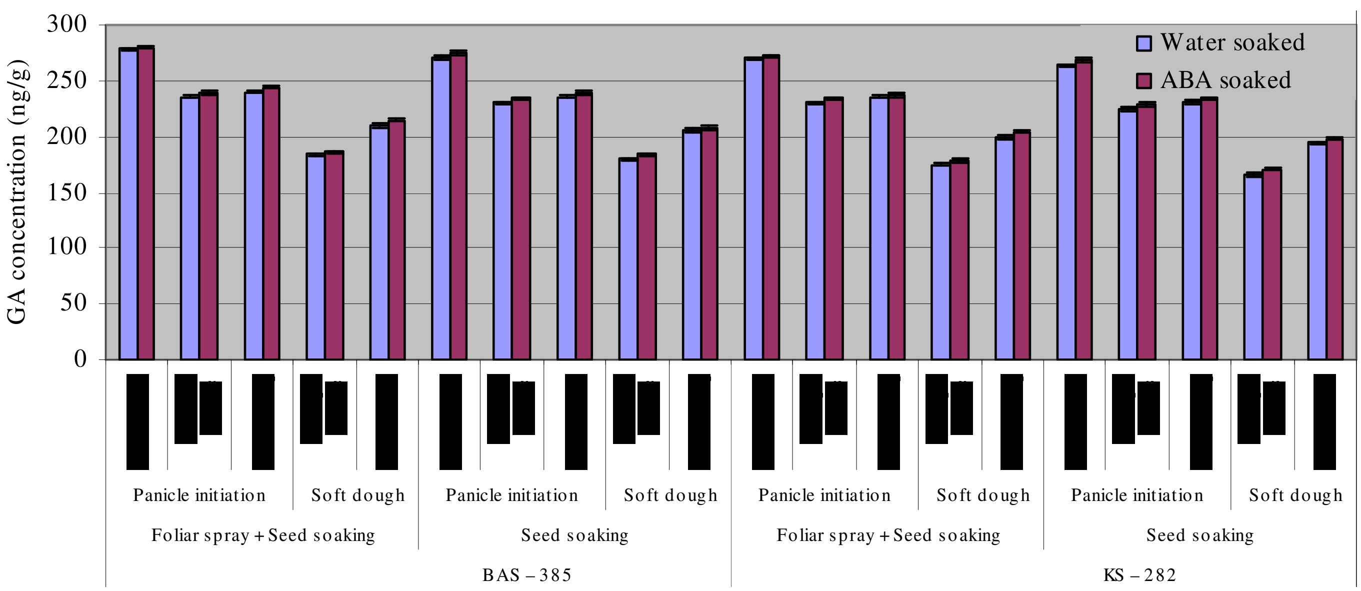


**Figure 4.** Effect of drought stress on GA content (ng/g) in grains of cv. BAS-385 and KS-282.

+ ABA foliar spray treatments and corresponding decrease due to drought was greater (16 and 35%) in GA leaves as compared to 10 and 24% decrease in IAA content at panicle initiation and soft dough stages, respectively.

ABA treatments were ineffective to ameliorate inhibitory effect of drought stress on GA content. GA is involved in increased rate of transpiration, water and ion flux. The ineffectivity of ABA on restoration of GA level appears to be one of the mechanisms for ABA induced water conservation in plants. Yang et al. (2000) reported reduction in GA accumulation in rice grains following application of ABA under drought stress. GA content was decreased in grains under water stress conditions (Yang et al., 2001; Xie et al., 2003). On rewatering, ABA seed soaking + foliar spray treatments and ABA foliar spray alone showed better recovery than that of drought alone. The basal level of ABA in leaves was less than that of GA and IAA in both cultivars, but cv. KS-282 exhibited relatively less ABA than cv. BAS-385. There was no significant difference in ABA content of grains of two varieties under unstressed conditions.

All the treatments with ABA increased ABA concentration under unstressed conditions in leaves and grains,

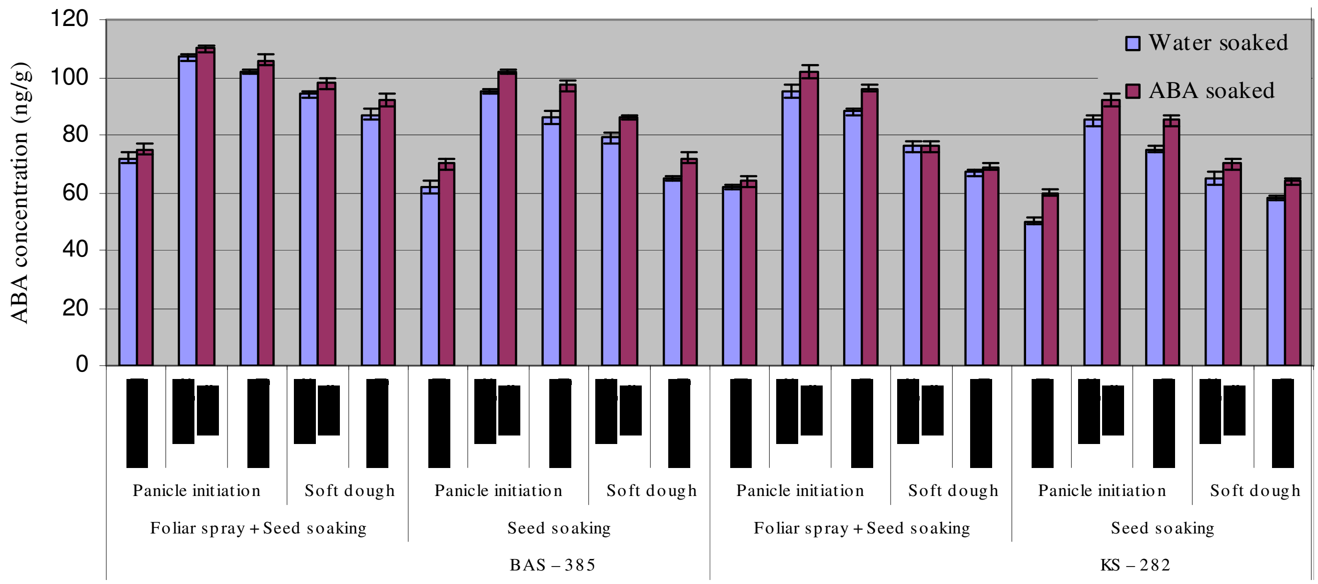


**Figure 5.** Effect of drought stress on ABA content (ng/g) in leaves of cv. BAS–385 and KS–282.

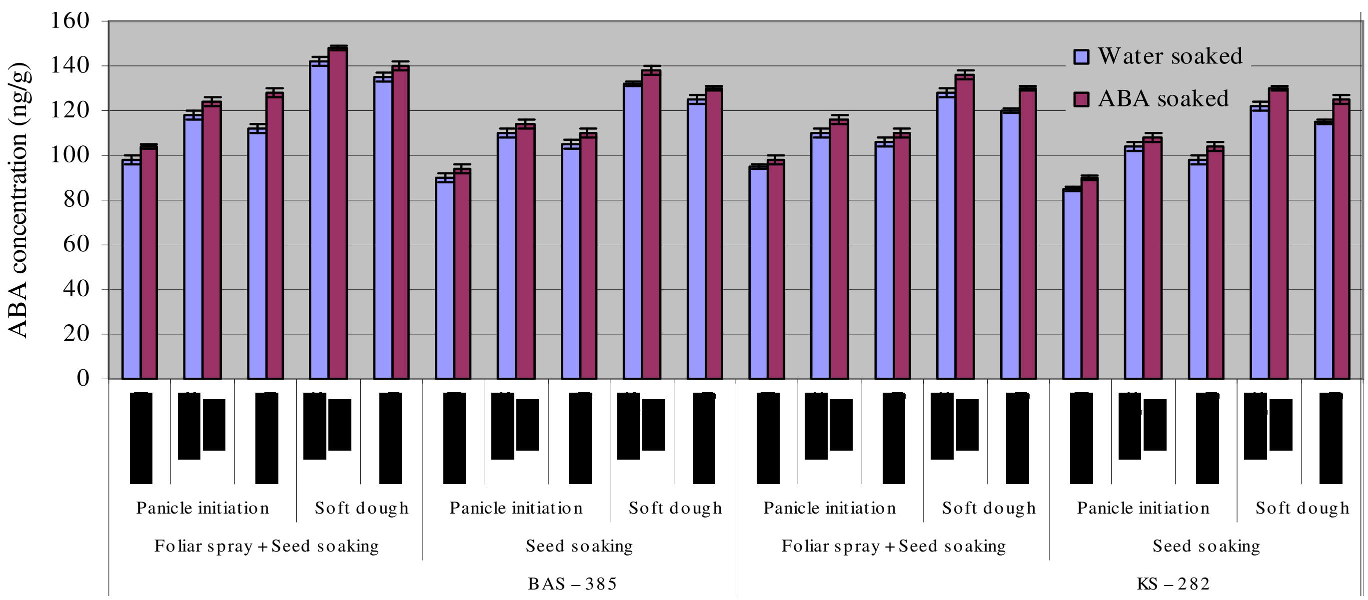


**Figure 6.** Effect of drought stress on ABA content (ng/g) in grains of cv. BAS-385 and KS-282.

but the stimulatory effect was less in ABA seed soaking treatment when compared to foliar spray. This increase in ABA may possibly be attributed to an induction in ABA synthesis. Pierce and Raschke (1981) observed that wilted leaves of *Phaseolus vulgaris* accumulated ABA and that could be due to stimulation of ABA synthesis.

Drought induced increases in the accumulation of ABA was higher in leaves at the panicle initiation stage but in grains it was greater at the soft dough stage (Figures 5 and 6). ABA seed soaking + foliar spray treatments significantly enhanced endogenous concentration of ABA both in leaves and in grains when compared to ABA seed soaking treatments. ABA is considered as a sensitive stress signal generated in grains under water deficit conditions (Davies and Zhang, 1991; Xie et al., 2003) and improved desiccation tolerance in cyanobacterial plants (Beckett et al., 2005; Bartels, 2005). This increase in ABA may possibly be attributed to the ABA induction of synthesis of ABA. Abscisic acid accumulation in leaves of plants under water deficit was greater than that of control (Yang et al., 2001, 2004).

On rewatering, the decrease in drought induced increase in ABA which was greater particularly in grain collected from plants receiving stress at panicle initiation

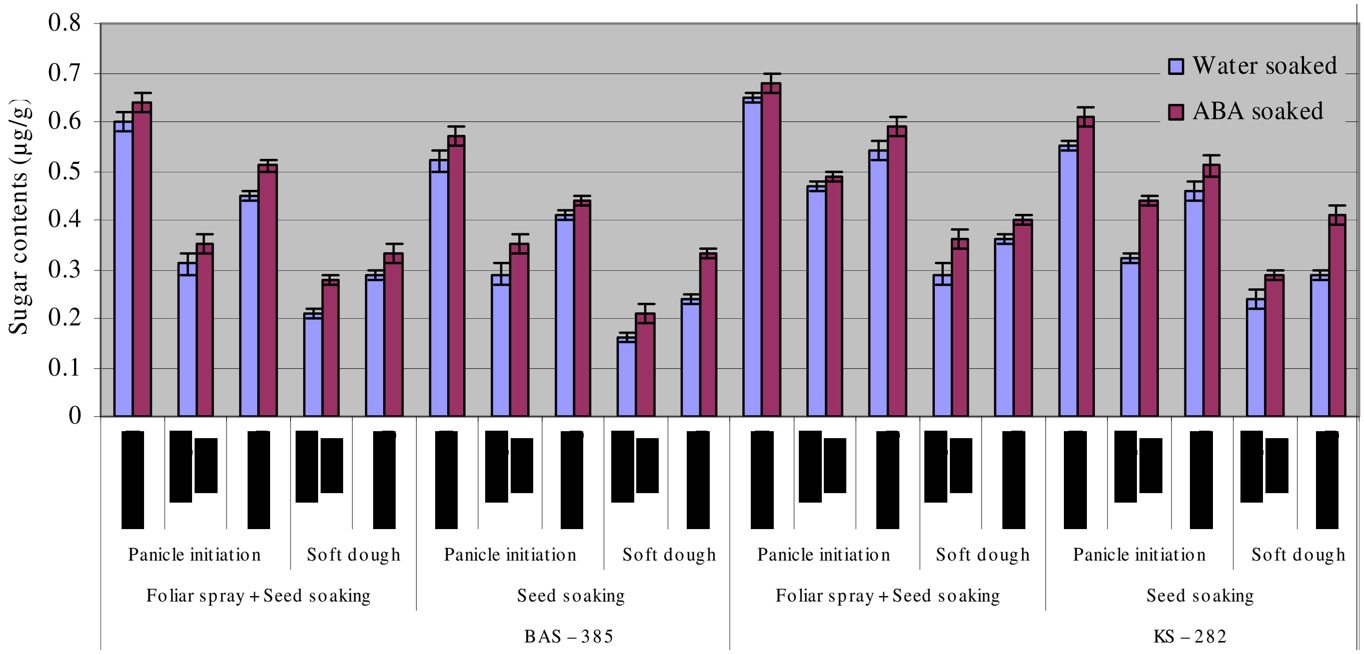


**Figure 7.** Effect of drought stress on sugar content (mg/g) in leaves of cv. BAS-385 and KS-282.

stage under ABA treatments. This may be due to higher level of growth promoting hormones viz., IAA, GA and CK, particularly in the developing grain. Kende and Zeevaart (1997) and Hansen and Grossmann (2000) reported that auxin and gibberellin regulate the process of plant grain development.

The basal level of ABA in leaves was less than that of GA and IAA in both cultivars but cv. KS-282 exhibited relatively less ABA than cv. BAS-385. There was no significant difference in ABA content of grains of two varieties under unstressed conditions.

## Sugar content

Under drought stress, ABA treatments have markedly increased sugar content under unstressed conditions both in leaves and grains (Figures 7 and 8). This increase may be due to the positive effect of ABA on assimilate translocation. Assimilate translocation to the developing seeds or fruits are reported to be under the control of ABA (Brenner and Cheikh, 1995; Yang et al., 1999, 2004).

Drought stress decreased accumulation of sugar markedly in leaves at soft dough stage and reduction of sugar content in grains was greater at panicle initiation stage (Figures 7 and 8). ABA treatments also showed decrease in sugar contents both in leaves and grains but the extent of decrease was significantly less than that of drought treatment. It may be suggested that accumulation of metabolite (sugars) may be related to regulatory functions of phytohormones (Mckersie and Leshem, 1994). Ahmadi and Bakker (1999) reported that ABA is involved in osmolyte regulation under moisture stress conditions. Mahajan and Tuteja (2005) reported that under severe drought, growth was inhibited by high concentration of ABA and sugar, whereas low concentrations promote growth.

ABA applications enhanced the percentage recovery of droughted plants. Increased rates of photosynthesis and higher chlorophyll content might cause accumulation of sugars due to ABA treatments (Dong et al., 1995; Ndung et al., 1997). Drought tolerance in plants is enhanced by ABA treatment possibly due to the accumulation of osmolytes such as sugars. Rewatering drought stressed plants may change hormonal concentrations (balance) and enhance the remobilization of pre-stored carbon in vegetative tissues to the grains of rice plant (Yang et al., 2001).

## Protein content

ABA induced protein content in leaves and grains of both cultivars under ABA seed soaking and ABA seed soaking + ABA foliar spray treatments. This may be due to positive role of ABA on protein accumulation. Guerrero and Mullet (1986) and Schmitz et al. (2000) reported that protein synthesis in developing seeds is induced by ABA.

Drought stress decreased accumulation of protein significantly in leaves at soft dough stage, whereas in grains, decrease in protein content was greater at panicle initiation stage (Figures 9 and 10). ABA seed soaking + foliar spray treatments also decreased protein contents both in leaves and grains but the extent of decrease was

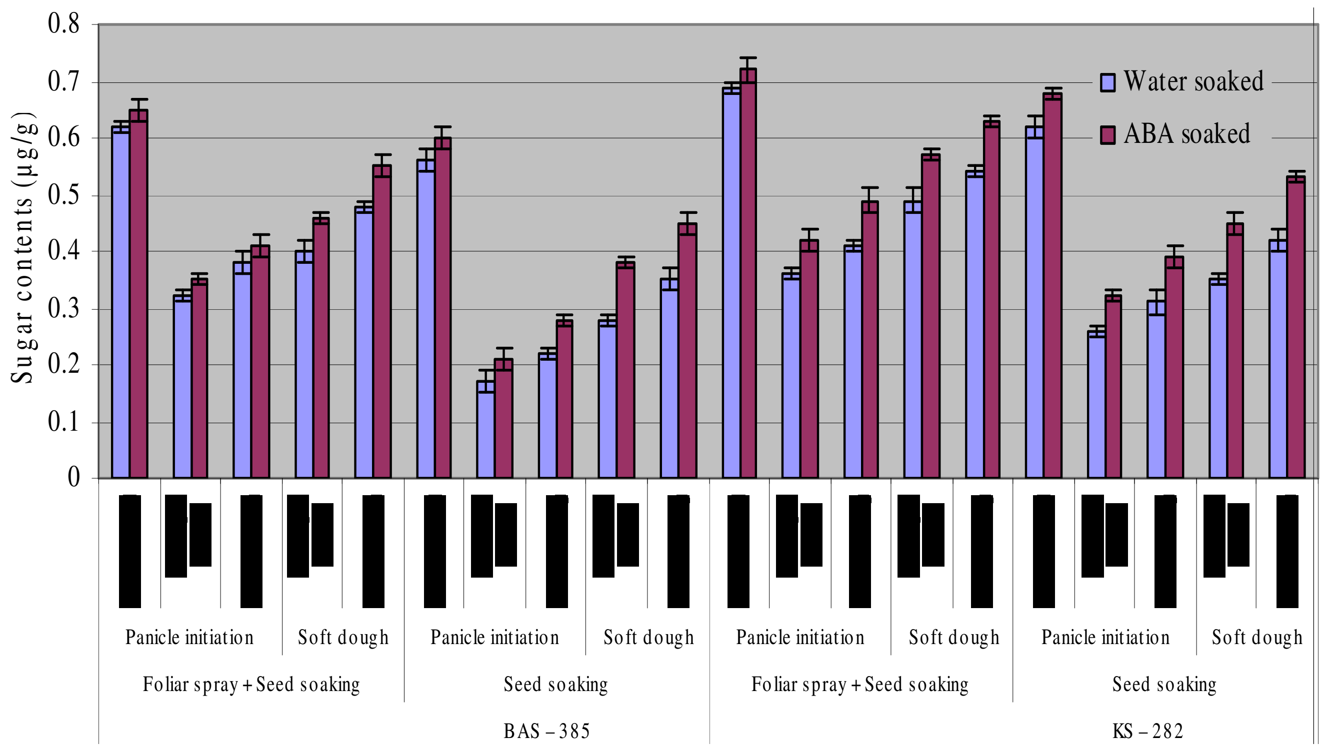


**Figure 8.** Effect of drought stress on sugar content (mg/g) in grains of cv. BAS-385 and KS-282.

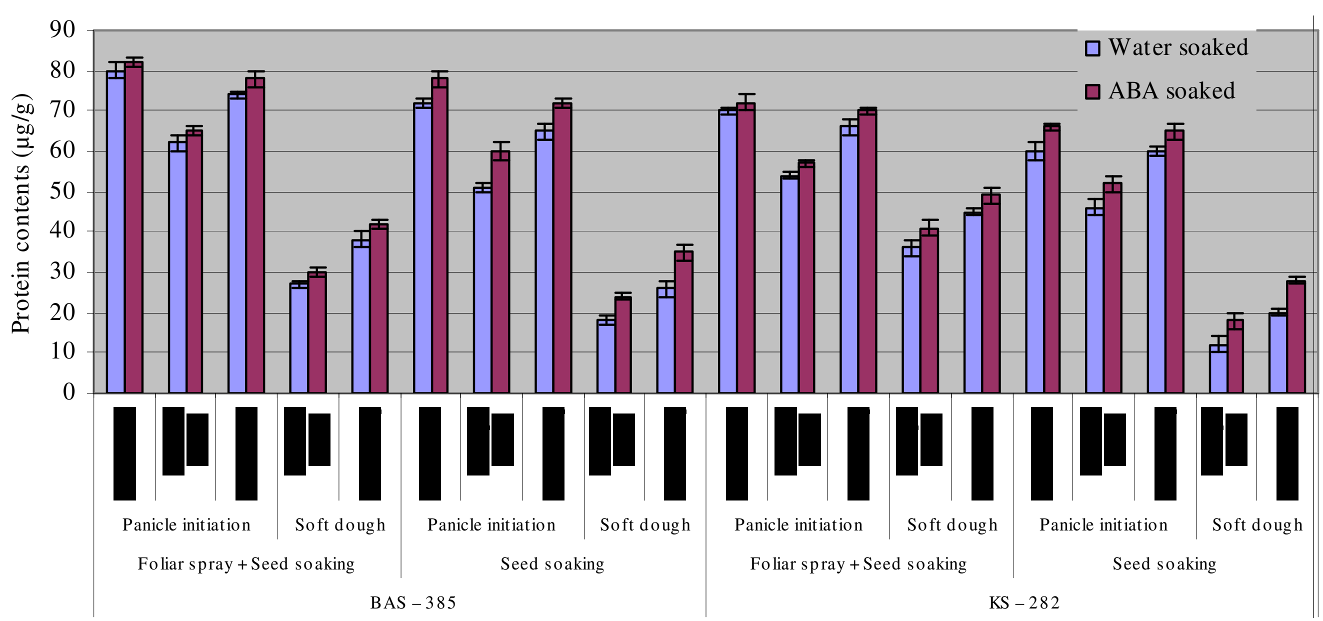


**Figure 9**. Effect of drought stress on protein content (mg/g) in leaves of BAS-385 and KS-282 cultivars.

less as compared to that of drought. It may be attributed that stress hormones ABA is involved in activation of specified genes/gene products linked to drought stress in rice plants for protein accumulation (Mundy and Chua., 1988). Zhang et al. (2001) reported that protein phosphorylation is enhanced under water stress due to increased concentration of ABA. Bartels and Sunkar (2005) and Ingram and Bartels (1996) investigated late embryogenesis abundant (LEA) proteins induced in vegetative tissues of plants in response to osmotic stress that may interact with carbohydrates to prevent cellular damage during dehydration.

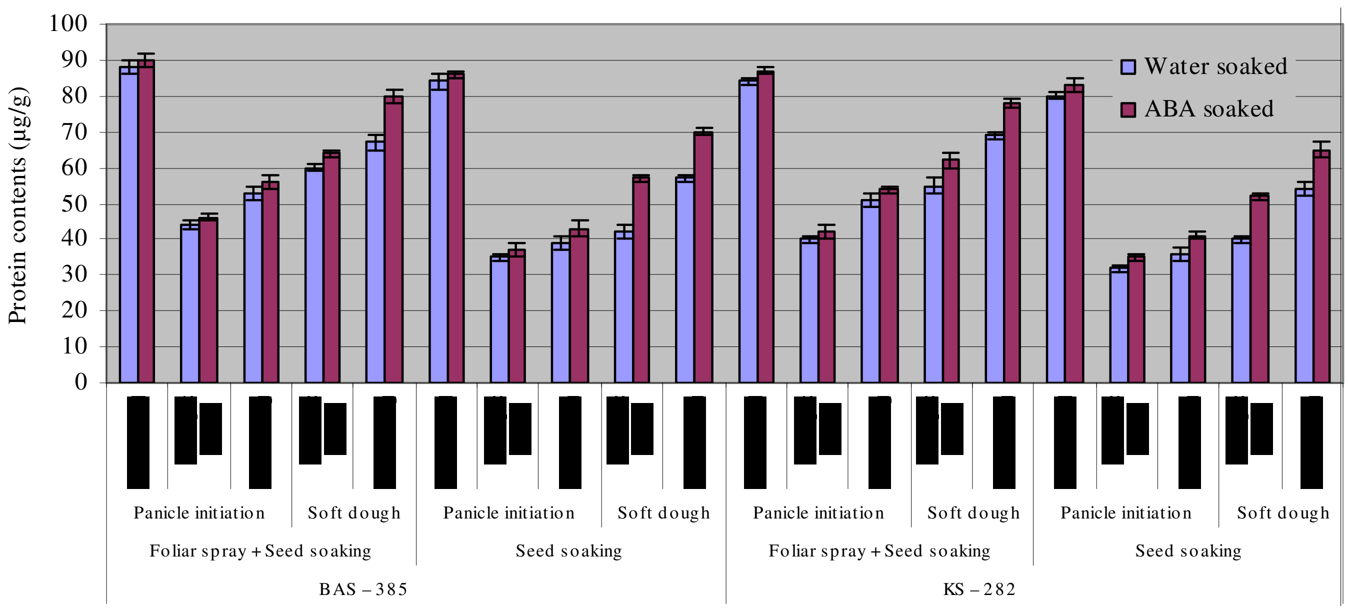


**Figure 10.** Effect of drought stress on protein content (mg/g) in grains of BAS-385 and KS-282.

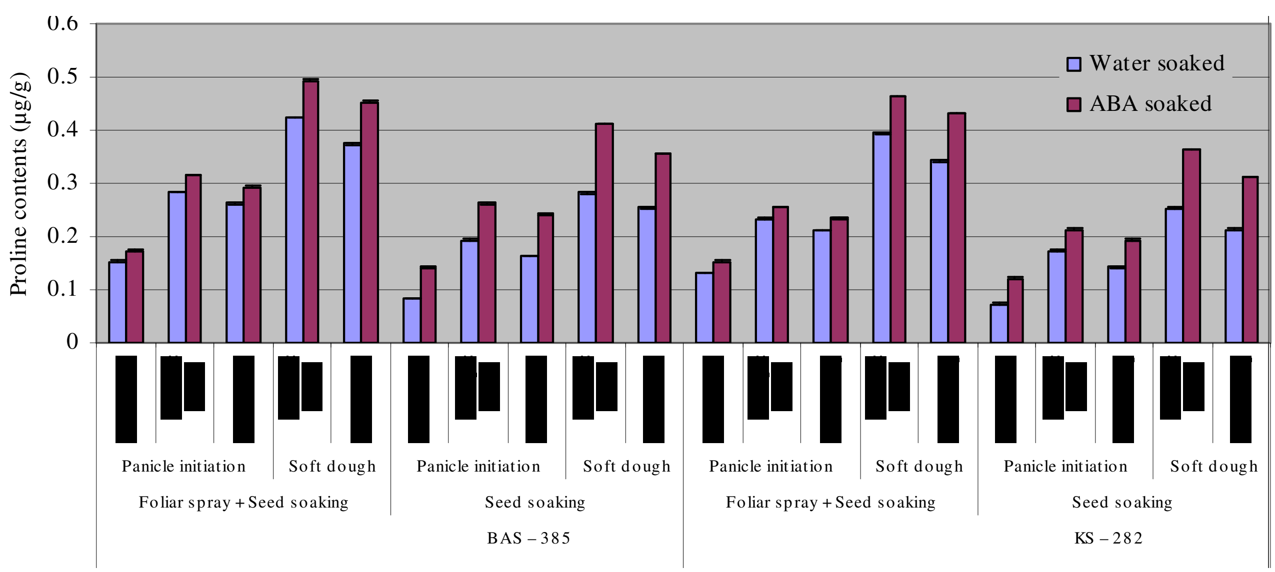


**Figure 11.** Effect of drought stress on proline content (mg/g) in leaves of BAS-385 and KS-282.

The recovery of leaf protein levels in drought stressed plants is more rapid at panicle initiation, while in grain, it was greater at the soft dough stage under both ABA seed soaking + foliar spray treatments.

## Proline content

ABA foliar spray and ABA foliar spray + seed soaking treatments had markedly increased proline content under unstressed conditions both in leaves and grains (Figures 11 and 12). This magnitude of increase was similar under drought stress. Under drought stress, in addition to its reported role as an osmoregulator, proline like other soluble organic compounds may also act as osmo-protectants (Kamelie and Lose, 1996, Rontein et al., 2002). ABA was considered to be involved in the accumulation of proline (Hare et al., 1999; Hose et al., 2000; Trotel Aziz et al., 2000; Nayyar and Walia, 2003; Verslues and Bray 2006), carbohydrates (Ahmadi and Baker, 2001) and other osmolytes in plants (Popova et al., 2000).

In leaves, proline content was less in the unstressed control of both the varieties in seed soaking treatment as

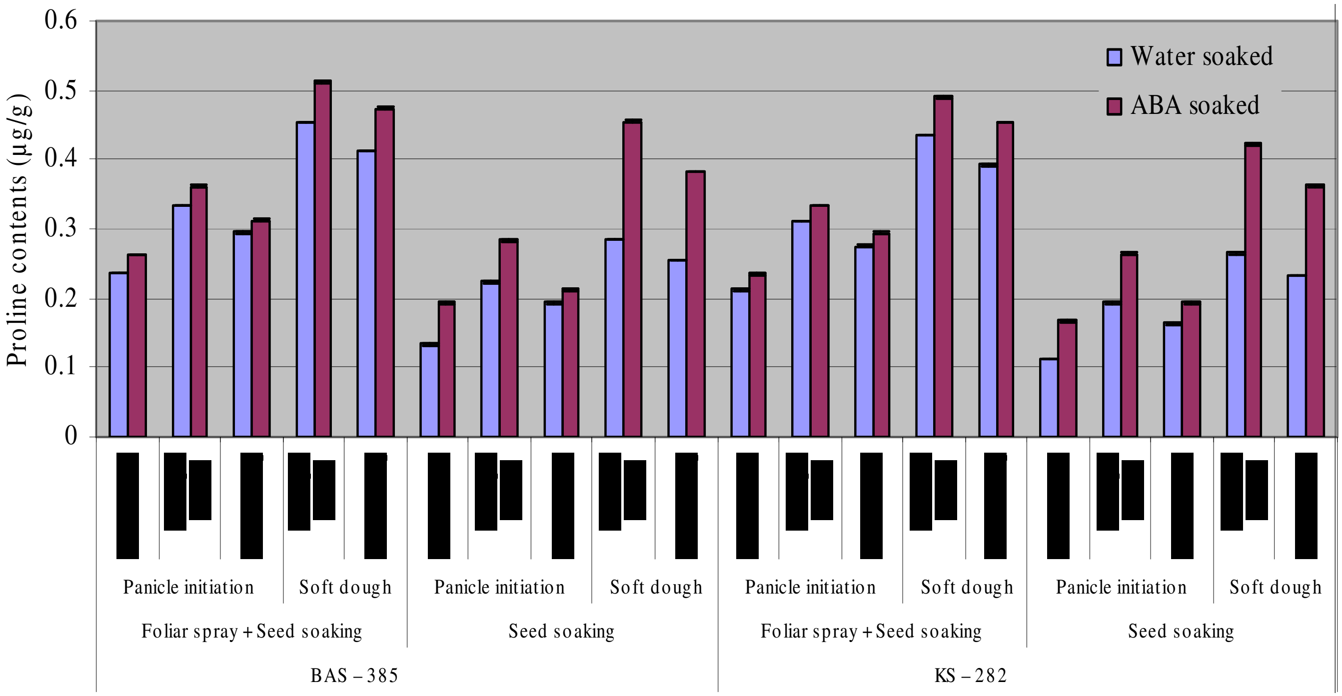


**Figure 12.** Effect of drought stress on proline content (mg/g) in grains of BAS-385 and KS-282.

compared to seed soaking + foliar spray. The cv. BAS-385 has relatively greater proline content in unstressed condition and also the drought induced proline content was greater at panicle initiation stage as compared to KS-282. Similar pattern of proline content was exhibited in grains of both the varieties.

Drought stress increased the accumulation of proline significantly both in leaves and in grains but the increase was more marked at the soft dough stage. ABA enhanced the accumulation of proline contents in grains more than in leaves (Figures 11 and 12). This increase may be due to role of ABA, which may stimulate proline accumulation under water deficit conditions. It was observed that marked increase in proline content is caused by ABA in excised leaves of rice (Chou and Keo, 1991). ABA was considered to be involved in the accumulation of proline (Hose et al., 2000; Nayyar and Walia, 2003) carbohydrates (Ahmadi and Baker, 2001) and other osmolytes in plants (Popova et al., 2000). Ashraf and Folad (2007) have demonstrated that proline accumulation increases the stress tolerance of plants. ABA foliar spray caused significant increase in proline levels when compared to other treatments (Bajji et al., 2001).

### Stomatal resistance in flag and penultimate leaf

Stomatal resistance was greater in flag leaf of both control and ABA treatment in both cultivars as compared to penultimate leaf. However, control (well watered) plants have less stomatal resistance in flag and penultimate leaves in both cultivars. ABA foliar spray treatments have significantly increased stomatal resistance under unstressed conditions both in flag and penultimate leaves (Figures 13 and 14). This increase may be due to the well defined role of ABA on stomatal functioning. ABA acts as a chemical signal involved in the regulation of stomatal functioning (Schulze, 1986; Davies and Zhang, 1991).

Drought stress increased stomatal resistance significantly in flag and penultimate leaves at panicle initiation stage as compared to soft dough stage (Figures 13 and 14). ABA seed soaking + foliar spray treatments significantly increased stomatal resistance over drought. The effect of drought was less at panicle initiation than that of soft dough stage in both varieties. Seed soaking treatment had relatively less decrease in stomatal resistance due to drought as compared to seed soaking + foliar spray in both varieties. As a plant experiences water stress, its stomata closes which then decreases or stops transpiration and photosynthesis depending on the severity of the stress (Taiz and Zeiger, 2002). This might be due to the fact that ABA can act as a long distance communication signal between water deficit roots and leafs, inducing the closure of stomata and reduce water loss through transpiration (Morgan, 1990, Davies and Zhang, 1991). ABA seems to be involved in the regulation of plant water balance and osmotic stress tolerance (Bonetta and Mccourt, 1998; Mahajan and Tuteja, 2005). Environmental conditions that increase the rate of transpiration also result in an increase in the pH of leaf sap, which can promote ABA accumulation and lead to reduction in stomatal conductance (Wilkinson and Davies

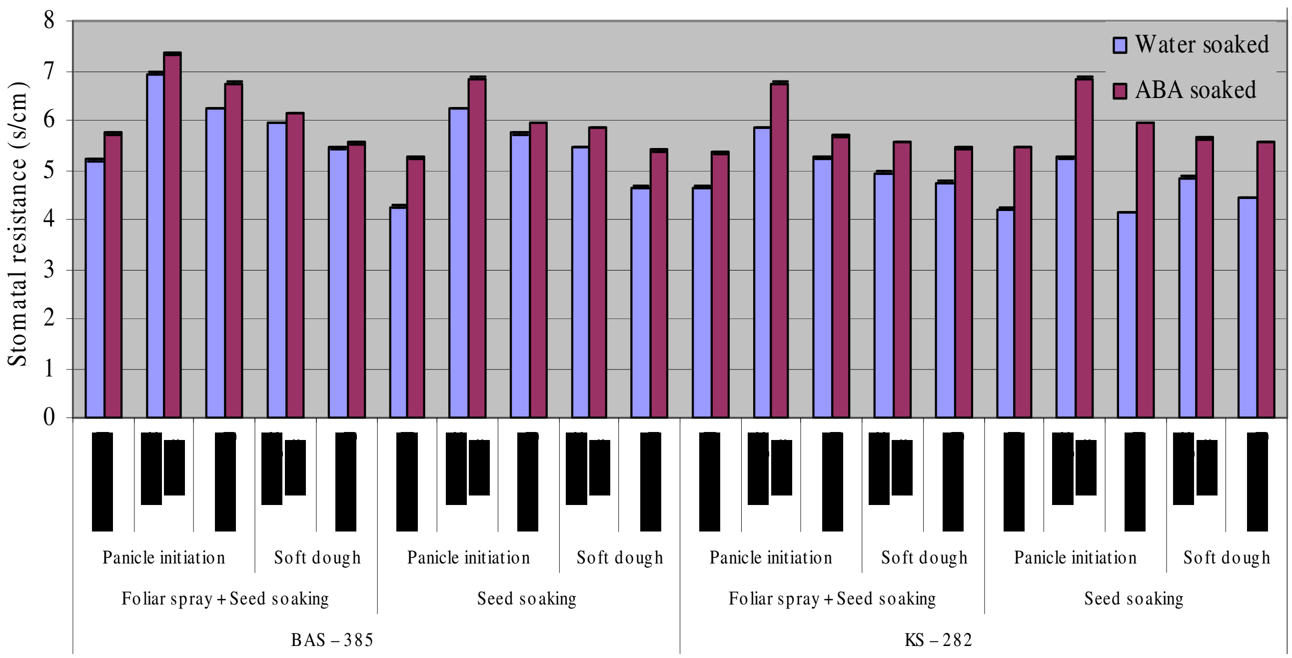


**Figure 13.** Effect of drought stress on stomatal resistance (s/cm) in flag leaf of cv. BAS-385 and KS-282.

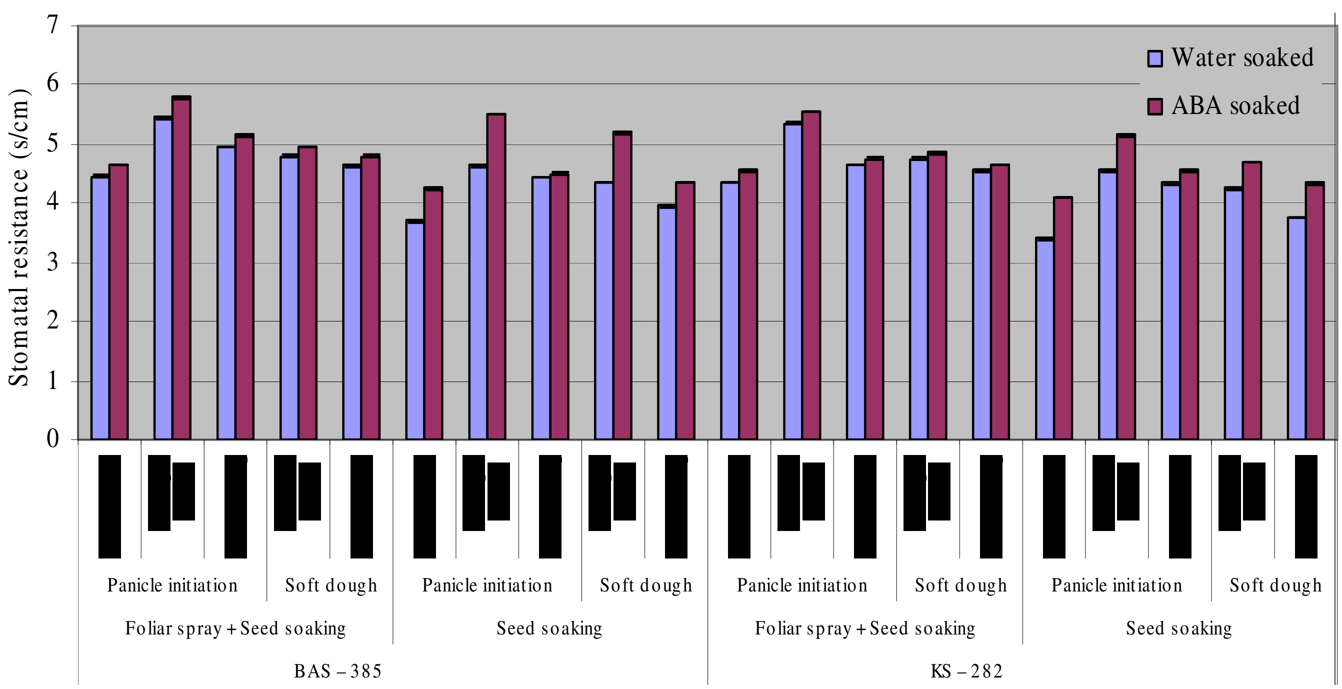


**Figure 14.** Effect of drought stress on stomatal resistance (s/cm) in penultimate leaf of cv. BAS-385 and KS-82.

2002; Davies et al., 2002).

## Rice plant biomass

Plant biomass of both cultivars (BAS-385 and KS-282) has been decreased markedly under both ABA foliar spray and ABA foliar spray + seed soaking treatments but its magnitude of reduction was less in ABA foliar spry + seed soaking treatments under unstressed as well as drought stress conditions (Figure 15). This less reduction may be due to synergistic effect of ABA foliar as well as

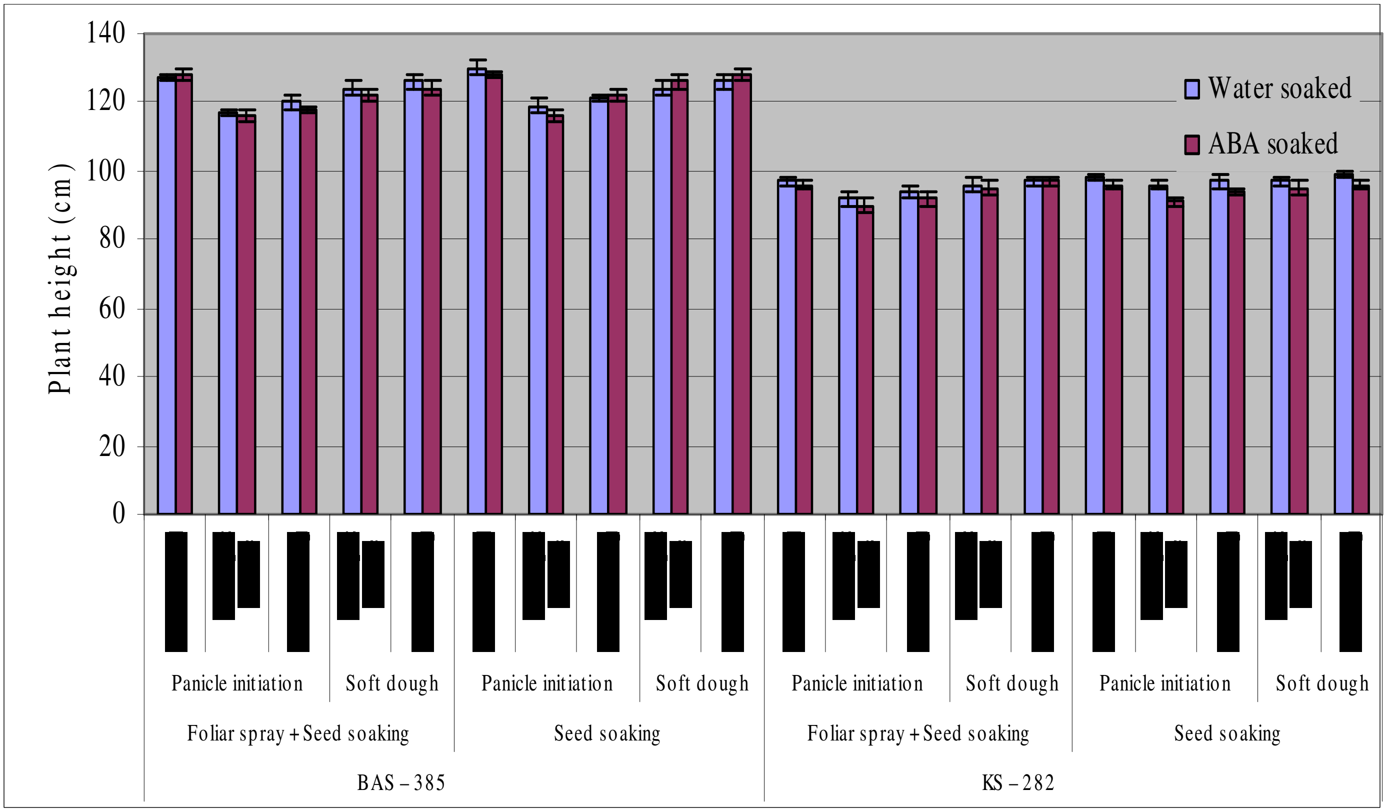


**Figure 15.** Effect of drought stress on biomass (gm / plant) in cv. BAS-385 and KS-82.

seed soaking treatments in both rice cultivars.

It has been deduced from Table 1 that KS-282, a coarse variety, showed more tolerance after induction of drought stress at panicle initiation and soft dough stages as compared to fine cultivar BAS-385. The effect was more pronounced in panicle size of KS-282 plants under both the stress conditions (at PI and SD stages) and 1000-grain weight at PI stage.

## Yield component of rice crop

Drought stress decreased plant height (Figure 16), productive tillers (Figure 17), panicle size (Figure 18), number of grains per panicle (Figure 19) and 1000-grain weight (Figure 20) at panicle initiation stage as compared to soft dough stage under ABA seed soaking alone as well as in combination with ABA foliar spray treatment in both cultivars. The recovery of plant from drought stress in case of plant height, productive tillers, panicle size and 1000-grain weight was more at soft dough stage.

ABA seed soaking treatment resulted in less decrease in productive tillers under drought and was better than combined effect of ABA soaking + foliar spray in both varieties. The magnitude of decrease was greater in KS-282 than BAS-385.

The drought induced decrease in grains number significantly in both cultivars but the magnitude of decrease was less in KS-282 as compared to BAS-385. Dietrich and co-workers (1995) reported the involvement of ABA, GA and IAA in regulation of grain development. Yang et al. (1999) and Wang et al. (1998) associated the poor grain filling with low IAA and ABA contents in rice grains.

## Conclusion

It is inferred that the mechanism of ABA induced tolerance under drought stress appeared to involve maintenance of water budget by affecting stomatal resistance and osmoregulation as observed by increases in proline accumulation. The ABA treatments were ineffective in ameliorating the inhibitory effects of drought stress on GA concentration because GA is involved in increased rate of transpiration, thereby ABA indirectly regulates water economy of plants by reducing GA concentration. It is inferred that beneficial effects of ABA can be optimized by genetic modification of endogenous ABA concentration produced under water stressed conditions and thereby improve crop production under drought conditions. Terpenoid analogue of ABA can replace ABA economically.

**Table 1.** Comparative assessment for effect of drought induction at Panicle Initiation (PI) and Soft Dough (SD) stages on the physiological/agronomic parameters of BAS-385 and KS-282. The values shown as compared to control unstressed plants.

| Cultivar | Panicle initiation | | | | | | | | | | Soft dough | | | | | | | | | | Grading |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Pl. height* | | Number of tillers | | Number of grain/pan | | Panicle size | | 1000-seed wt | | Pl. height | | Number of tillers | | Number of grain/pan | | Pan size | | 1000-seed wt | | |
| | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | ABA* | ABA + FS** | |
| BAS-385 | -- | -- | 0 | --- | --- | -- | --- | - | -- | - | - | - | 0 | --- | --- | -- | 0 | --- | 0 | --- | Less tolerant |
| KS-282 | - | - | ---- | ----- | --- | ---- | - | ++ | - | ++ | + | 0 | --- | ---- | -- | --- | +++ | - | 0 | - | More tolerant |

*Pre-sowing ABA seed soaking + drought at panicle initiation and soft dough stage; **Pre-sowing ABA seed soaking+ foliar spray at tillering stage + drought at panicle initiation and soft dough stage;. - = Decrease; + = increase; 0 = no change. The number of + or - indicate the magnitude of increase or decrease.

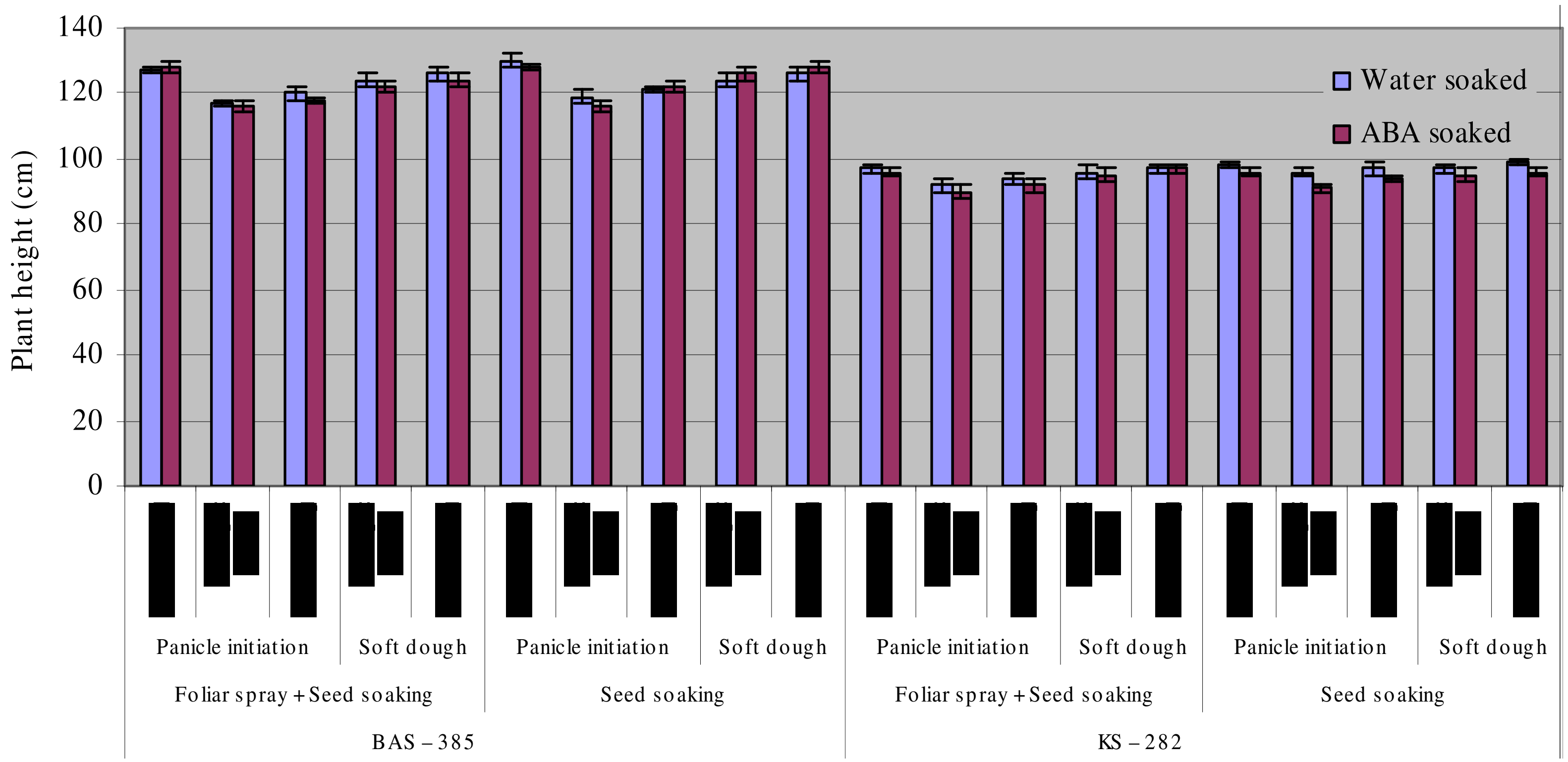


**Figure 16.** Effect of drought stress on plant height (cm) in cv. BAS-385 and KS-82.

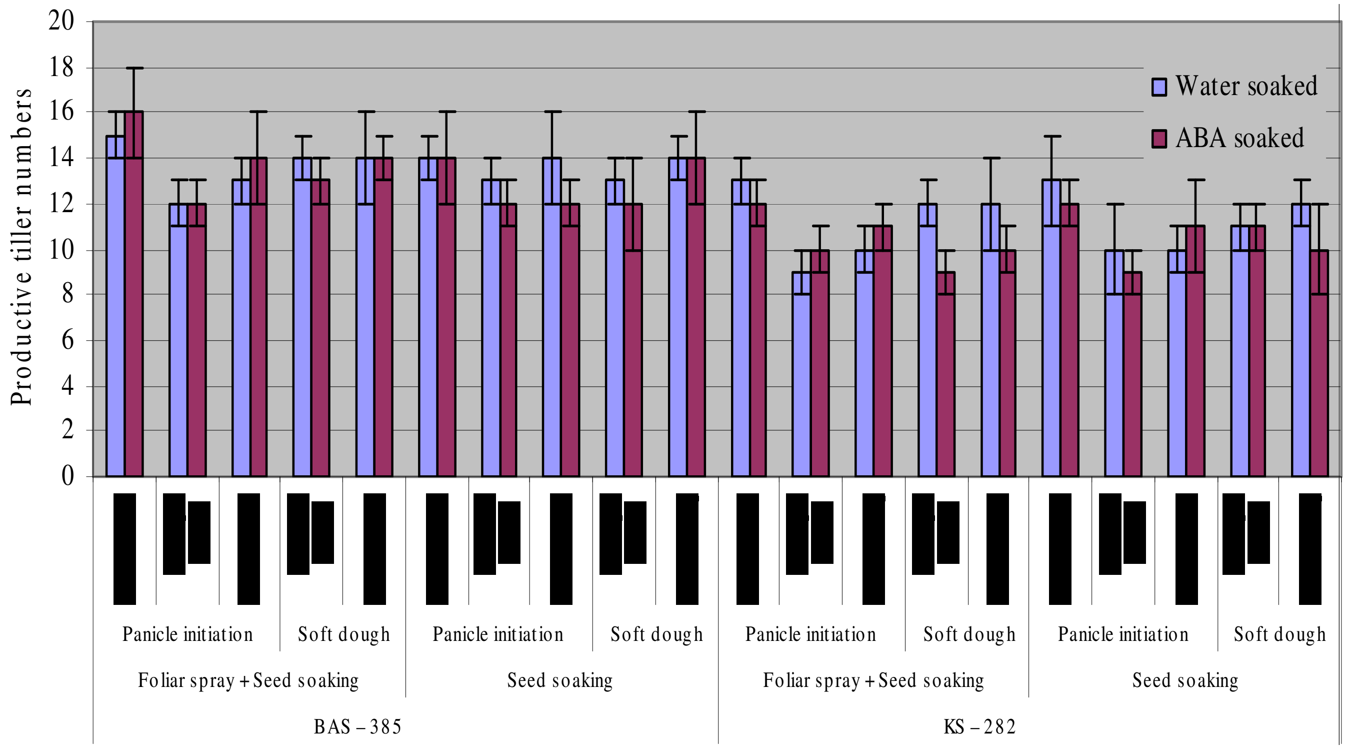


**Figure 17.** Effect of drought stress on Productive tillers in cv. BAS-385 and KS-82.

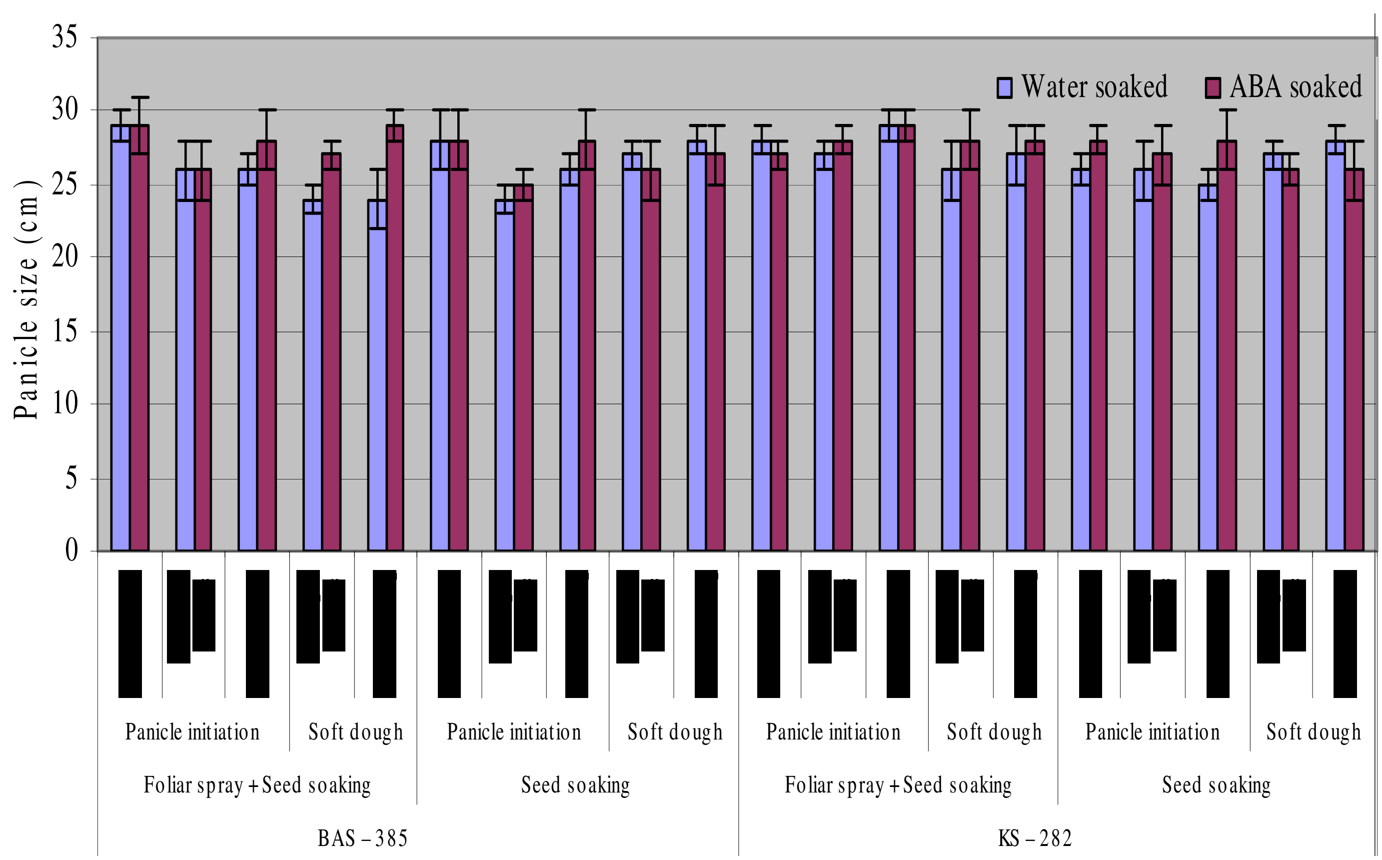


**Figure 18.** Effect of drought stress on panicle size (cm) in cv. BAS-385 and KS-82.

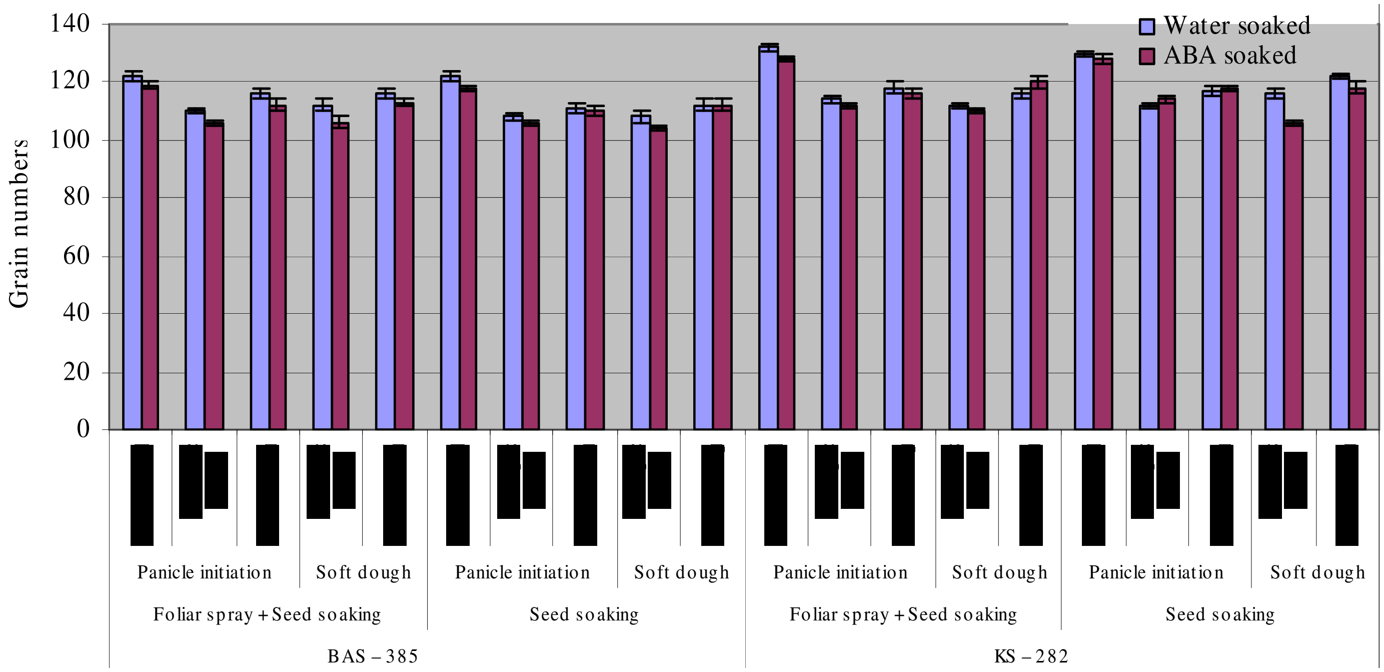


**Figure 19.** Effect of drought stress on number of grains per panicle in cv. BAS-385 and KS-82.

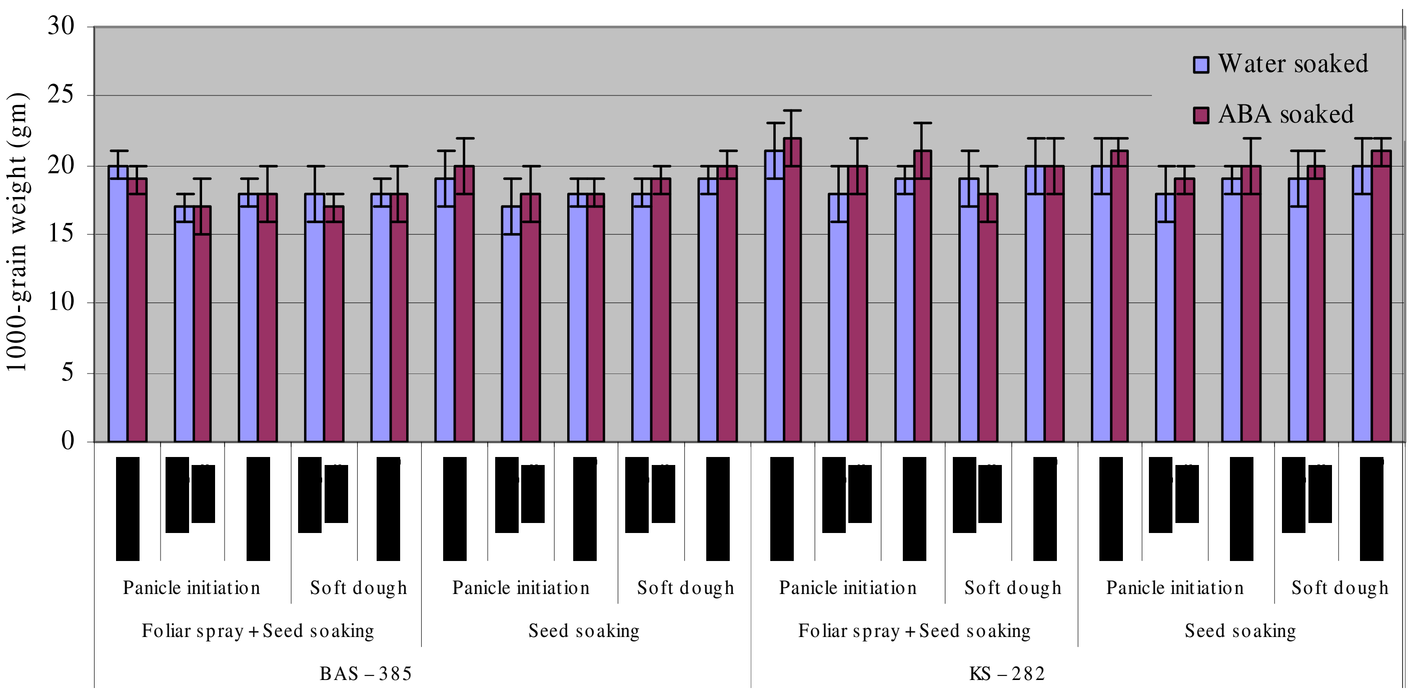


**Figure 20.** Effect of drought stress on 1000-grain weight (gm) in cv. BAS-385 and KS-82.

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