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The Effects of Drought Stress on Assimilate Availability and Metabolism in the Source and Sink Organs of Common Bean (*Phaseolus vulgaris* L) Genotypes

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Abstract

Changes in carbohydrate status and metabolism in the source and sink organs determine rate of growth and yield of plants subjected to drought stress. The objective of this study was to assess the effect of post-flowering drought stress on assimilate synthesis at source level and availability of the assimilates for metabolism in the reproductive sink organs of common bean (*Phaseolus vulgaris* L.) genotypes differing in degree of drought resistance. A drought-resistant inbred line (SEA 15) and a drought-susceptible cultivar (BrSp) were grown under non-stress and drought stress commenced at early pod-filling stage. Plants were raised in a vegetation hall during the summer of 2005. Drought stress reduced the seed yields of BrSp and SEA 15 by 53 and 30%, respectively. Harvest index of the susceptible genotype decreased by ca. 29%, whereas no effect of drought was found for the partitioning index in the resistant genotype implying marked differences in sink strength at whole plant level between the genotypes. Drought stress did not affect the concentration of sucrose in leaves and seeds of SEA 15 during most part of the stress period. On the contrary, the stress caused 18 to 30 and 29 to 47% reductions in leaf and seed sucrose concentrations of BrSp, respectively. Relative to control treatments, drought stress decreased seed starch accumulation of BrSp throughout the stress period (by 16 to 18%) whereas the decrease (by 20%) was found only at 20 d stress for SEA 15. The findings revealed that the underlying differences in sink establishment and yield of the bean genotypes differing in degree of drought resistance reside primarily in the capacity of the source to supply assimilates (i.e. source-strength) under drought conditions.

Introduction

As much as 60% of common bean (*Phaseolus vulgaris* L.) production in the developing world occurs under conditions of significant drought stress (Graham and Ranalli 1997). Consequently, the average global yield of beans remains low (<900 kg ha^{-1}) (Singh 2001). Limitations to crop yields are often sought in either source or sink restrictions. The source activity, which determines the availability of assimilates and the sink strength, which determines the ability of sink organs to import and utilize assimilate are the two processes involved in determining yield of a crop (Egli and Bruening 2001; Ho 1988). At whole plant level, the differences in drought resistance among drought-resistant and susceptible genotypes are related to the ability to accumulate biomass, remobilization of stored biomass to reproductive organs and the subsequent capacity to establish new reproductive sinks (Koç et al. 2003; Chaves et al. 2002).

Drought stress (leaf relative water content drops below 95%) decreases photosynthetic rate thereby disrupting carbohydrate metabolism in leaves (Kim et al. 2000). As a consequence, the amount of assimilates available for export to the sink organs may be reduced leading to an increased rate of reproductive abortion. In drought-stressed wheat (Wardlaw 2002), smaller/loss of kernel set was correlated with the extent of loss in photosynthate influx into kernels. As sucrose is the principal form of photosynthate for long-distance transport to sink organs, its concentration in leaves represents the current availability of assimilate for reproductive development (Westgate and Thomson 1989). Any effect of drought on synthesis, partitioning, export and utilization of sucrose would modify availability of the assimilate at source level (Huber 1989). In several plant species subjected to drought stress, leaf starch and sucrose concentrations decreased rapidly and became close to zero, whereas the concentrations of glucose and fructose significantly increased (Lawlor and Cornic 2002). The resulting high concentrations of hexose may be involved in a feedback regulation of photosynthesis (Chaves et al. 2002).

Drought stress can also affect carbohydrate metabolism in plant reproductive organs (Liu et al., 2004). Sucrose concentrations in reproductive structures of drought-stressed plants, i.e., in maize ovaries and rice (*Oryza sativa* L.) anthers, were found to be higher or at least similar to those of the well-watered controls (Setter et al. 2001; Sheoran and Saini 1996). The results imply that rather than sucrose concentration *per se*, the capacity for sucrose utilization may be affected by drought stress. In drought-stressed maize, accumulation of sucrose in young ovaries coincided with a cessation of ovary growth and a decrease in the concentration of hexose (Zinselmeier et al. 1999). In line with these findings, the extent of changes in carbohydrate status and metabolism in source and sink organs of common bean cultivars differing in drought resistance may determine the success of their reproductive sink establishment, growth and ultimately yield. The objective of this study was to assess the effect of post-flowering drought stress on assimilate synthesis at source level and availability of the assimilates for metabolism in the reproductive sink organs of common bean (*Phaseolus vulgaris* L.) genotypes differing in degree of drought resistance.

Materials and Methods

Plant material

A drought-resistant inbred line (SEA 15) and a susceptible bean cultivar (Brown Speckled hereafter referred as BrSp) were used in this study. The adapted cultivar (BrSp) was chosen among varieties developed by the National Bean Research Program of Ethiopia for wider adaptations to different agro-ecological conditions of the country. The inbred line (SEA 15) was obtained from the bean research program of the International Center for Tropical Agriculture (CIAT). Previous studies have demonstrated that the resistant genotype possesses an adequate level of resistance to drought stress under field conditions (CIAT, 2002).

Experimental treatments and design

The two genotypes were grown under non-stress (control) and drought stress initiated at early pod-fill stage during the summer of 2005 at Experiment Station of the University of Giessen, Germany. Drought stress was imposed by withholding the amount of water applied in order to keep the soil moisture level at about 30% of the maximum water-holding capacity (WHC). For non-stressed (control) treatments, the soil moisture was maintained at 70% of the maximum WHC until the plants were harvested. The daily minimum and maximum temperatures (mean ± S.D.) during the growth period of 2005 were 26.2±5.1 and 23.8±4.8 °C, respectively. The daily average temperature during same period was 19.3±4.1.

Seeds of the test genotypes were grown in *Ahr* pots filled with 13 kg of Kleinlindener soil. At the time of planting, the soil was fertilized with Blaukorn (12.0% N, 5.2% P, 14.1% K, 1.2% Mg and 6.0% S). Eight seeds per pot were initially sown and later thinned to four plants when the first trifoliate leaves were unfolded. Plants were raised in a vegetation hall. The pots were weighed daily and watered to restore the appropriate moisture by adding a calculated amount of water. The treatments were laid in a completely randomized designed with four replications.

Data collection

Seed yield (g plant^{-1}) was calculated as a product of the three yield components (number of productive pods per plant, number of seeds per pod and seed weight). Hundred seed weight (HSW, g) was determined on 100 seeds randomly sampled from all plants harvested per pot. Harvest index (HI) was calculated as the proportion of seed weight to the above-ground dry weight (stem + leaves + pod + seed) at harvest.

Chemical analysis

For sugar and starch analyses, leaf, pod and seed samples were obtained from the harvests of all the four plants made at 5, 10 and 20 d after the commencement of drought stress. The various plant parts were dried separately at 80^{o}C for 48 h and finely ground materials were used for the chemical analyses.

Sugars: Three-hundred mg ground plant material was weighed into a 50 ml volumetric flask and 30 ml of double-demineralized water was added. The material was then extracted by incubating in a shaking water bath at 60°C for 30 min. The flask was quickly cooled on ice, and filled up to the mark with double-demineralized water followed by filtration with (blue-band) filter paper (Faltenfilter 595$^{1/2}$, Scheicher and Schüll Co., Dassel, Germany). Sugars (sucrose, glucose and fructose) were determined by using enzymatic test kits (Boehringer, 1984) and absorbances of the solutions were read at 340 nm.

Starch: Starch determination was performed following enzymatic assay procedure using the starch determination kit from Boehringer (Boehringer Mannheim, 1980). Homogenized ground seed and leaf samples of 300 mg were weighed into Erlenmeyer flasks, and 20 ml of dimethylsulfoxide and 5 ml HCl (8 mol/l) were added. The sealed flask was then incubated for 30 min at 60°C in a shaking water bath. The sample solutions were cooled quickly to room temperature and approximately 50 ml water was added. The pH was adjusted to 4 – 5 with sodium hydroxide (5 M) under vigorous shaking. The solution was then transferred to a 100 ml volumetric flask, rinsed with water, filled up to the mark with water and filtered using Faltenfilter 595$^{1/2}$ (Scheicher and Schüll Co., Dassel, Germany).

Free amino acids: Free amino acid concentrations were determined by quantifying α-amino N using the Ninhydrin method. Ground dry materials (100 mg) of various plant parts were extracted with 20 ml phosphate buffer in a 100 ml poly flask with an end-over-end shaker for 1 h. After filtration of the extract (Faltenfilter 595$^{1/2}$, Scheicher and Schüll Co., Dassel, Germany), 0.4 ml of the sample solution was mixed with 4 ml citrate buffer and 4 ml ninhydrin solution in a reagent glass and incubated for 15 min in a water bath at 100°C. After cooling down the reagent glass in water for 5 min, the solution was added into a micro cuvette and α-amino N concentration was determined by means of a spectrophotometer at a wavelength of 570 nm. A calibration curve was made with L-glutamine, which was prepared in the same way with the sample solution, and data were expressed in nmol α-amino-N kg $^{-1}$ dry weight (DW).

Protein: The nitrogen concentration was determined by means of sulphuric acid digestion in a Büchi K-324 (BÜCHI Labortechnik AG, Switzerland). Ground leaf samples of 500 mg were digested by adding 20 ml of H_2SO_4 and a Kjeldhal Cu–Se catalytic pill. The digestion process was left to run its course until the samples were clarified. The samples were then diluted to 50 ml with distilled water. In order to determine the nitrogen concentration, 5 ml of ionic strength adjuster was added to 5 ml of measuring solution. Measurements were performed with an ammonia-selective electrode using 0.1 m*M* of ammonium chloride as a standard. The nitrogen content quantified by this method was multiplied by an approximate factor of 6.25 to estimate the crude protein content of the bean seed samples.

Data analysis

Data were analyzed using the statistical package MSTAT-C, developed by Michigan State University (MSTAT-C, 1989). Data were subjected to analysis of variance (ANOVA) to determine significant differences among treatments for various parameters. Means of the treatments that exhibited significant differences were separated using the least significant difference (LSD) test. The differences of means between control and drought-stressed treatments were tested for statistical significance using the t-test. For all analyses, a P-value of less than 0.05 was interpreted as statistically significant.

Results and Discussion

Effects on seed yield and yield components

Drought stress commenced at early pod-filling stage and kept for 20 d resulted in 53 and 30% reduction in seed yields of BrSp and SEA 15, respectively (Fig. 1). The decrease in seed yield under drought stress was primarily due to the significant reduction in number of seeds per plant (Table 1). The smaller numbers of seeds per plant under stress for BrSp (20 under drought vs. 41 under control) were ascribed to the significant decrease by about 26% in the numbers of pods per plant and ca. 28% reduction in numbers of seeds per pod. For SEA 15, however, the reduction in the number of seeds per plant owing to drought was due mainly to ca. 25% less number of productive pods retained per plant. The seed weight of both genotypes remained relatively stable under the contrasting soil moisture regimes (Table 1).

Table 1. Seed yield and yield components of two common bean genotypes 20 d after the commencement of drought stress at pod-filling stage.

Treatment		No. pods (plant^{-1})	No. Seeds (pod $^{-1}$)	No. Seeds (plant $^{-1}$)	100-seed wt. (g)
Br Sp	Control	12.8±0.1 ^{b}	3.18±0.16 ^{b}	40.8±2.5 ^{c}	21.0±1.7 ^{bc}
	Stress	9.5±0.5 ^{c}	2.29±0.20 ^{c}	21.4±1.1 ^{d}	18.4±0.9 ^{c}
SEA15	Control	15.1±0.3 ^{a}	4.10±0.14 ^{a}	62.1±2.5 ^{a}	24.0±0.9 ^{b}
	Stress	11.3±0.8 ^{b}	3.59±0.14 ^{b}	40.4±2.2 ^{b}	25.7±0.8 ^{a}

Means in the same column having same letters in common are not significantly different according to LSD test at 5% level of probability. Data are the means±S.E. of four replications.

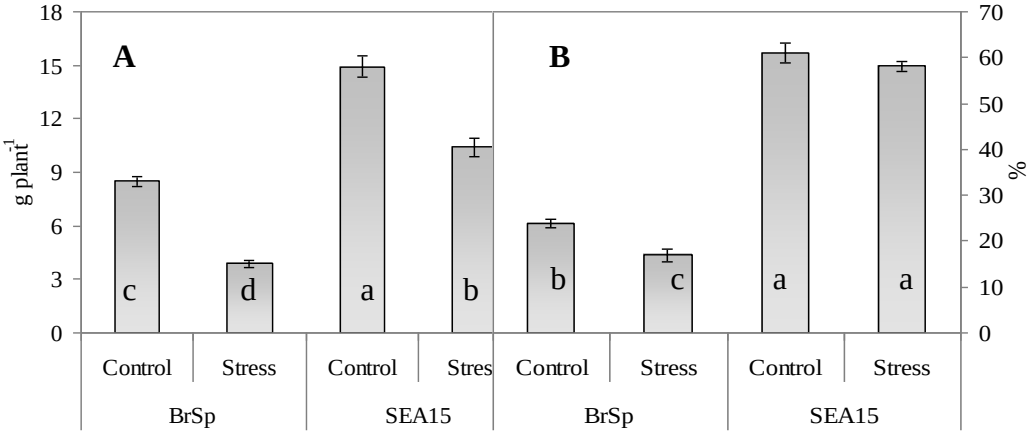

Fig. 1. Seed yield (A) and harvest index (B) of two common bean genotypes 20 d after the commencement of drought stress at pod-filling stage.

Mean-values having same letters in common are not significantly different according to LSD test at 5% level of probability .Vertical bars show ±S.E. of four replications.

Among the yield attributes, the number of pods per plant destined for final harvest to a large extent determined the differences in yielding levels of the tested genotypes under drought conditions. Relative to the initial number of pods formed prior to the commencement of drought stress, the number of productive pods retained per plant at 20 d stress was considerably more reduced for BrSp (68%) than for SEA 15 (51%) (Table 1). The stress also reduced the harvest index of the susceptible genotype, BrSp by about 29% whereas SEA 15 maintained comparable harvest indices under the contrasting soil moisture regimes (Fig. 1).

The reduction in seed yield per plant due to drought stress imposed at reproductive stage was due to the adverse effect of the stress on individual yield components. Consistent with reports on other legumes including common bean (Leport et al. 2006; Boutraa and Sanders 2001), the numbers of pods per plant followed by seeds per pod were the most affected yield components under drought stress (Table 1). Drought-induced abortion of pods for BrSp and SEA 15 were approximately two-third and one-half of the initial pod set (data not presented). In line with the suggestions of Daie (1996), the higher rate of pod abortion found for BrSp (relative to SEA 15) could be due to limited assimilate supply under drought conditions (Fig. 2).

The relatively smaller harvest index found for BrSp under both growth conditions (Fig. 1) demonstrates that the drought-susceptible genotype has inherently lower sink strength than SEA 15. Losses in vegetative biomass owing to drought stress occurring during grain filling coupled with important gains in harvest index have previously been reported for drought-resistant genotypes of several crops including some legumes (Chaves et al. 2002). According to Zhang et al. (2005), mobilization of reserves is dependent on sink strength, which varies with the genotype and is affected by the environment (e.g. water availability). In line with this and other available

reports (e.g. Monneveux et al. 2005), it is suggested that the mechanisms underlying differences in drought resistance (yielding ability under drought stress) of the bean genotypes are primarily related to the selections made for efficient biomass partitioning to reproductive structures rather than biomass accumulation ability *per se*.

Effects of drought stress on assimilate metabolism in the source and sink organs

Assimilate availability at source level: source strength

Leaf sugar concentrations of the two bean genotypes were differentially affected under drought stress initiated during the reproductive phase. For the drought-resistant genotype, SEA 15, leaf sucrose concentration remained unaffected except at 10 d stress (Fig. 2A). On the contrary, a consistent decline by ca. 18 - 30% relative to the non-stressed plants was found for the drought-stressed BrSp (Fig. 2A). Leaf hexose sugars (glucose + fructose) concentrations of BrSp decreased (although significant only at 20 d stress) due to drought whereas the concentration showed fluctuations for SEA 15 (Fig. 2B). Leaf total sugar (sucrose + hexoses) concentrations of SEA 15 were comparable between the contrasting soil moisture regimes, whilst the stress caused 14 - 28% reduction for BrSp (Fig. 2C).

As pointed out earlier, drought stress differentially affected the availability of sucrose in the leaves of the bean genotypes (see Fig. 2A). Nevertheless, concentration of the assimilate in the pods of both bean genotypes was comparable between drought-stressed and non-stressed plants (Fig. 5A). Previous studies have demonstrated a linear relationship between sucrose availability in the source and rate of export to sink organs (Huber et al. 1984). Corresponding to these reports, comparable pod sucrose concentrations found between drought-stressed and non-stressed SEA 15 plants reflected the availability of the assimilate at source level presented in Fig. 2A. In BrSp, similar level of sucrose found in the pods of stressed plants with those grown under non-stress conditions could be due to the inhibition of the hydrolysis of incoming sucrose, because hexose sugar concentration in the same reproductive organ was significantly lowered under drought stress (Fig. 5B). Sucrose accumulation with a concomitant increase in sucrose to hexose sugars ratio has been observed previously in soybean pods (Liu et al. 2004) and maize ovaries (Setter et al. 2001) of drought-stressed plants.

In sucrose-transporting plants such as beans, leaf sucrose concentration represents the current availability of assimilates for reproductive development (Westgate and Thomson 1989). Subjecting the bean genotypes to drought stress during the pod-filling stage did not consistently alter leaf sucrose concentration of SEA 15 (except at 10 d stress), whereas consistent reductions were found for BrSp at all durations of stress monitored (Fig. 2A). Consistent with our findings for the drought-susceptible genotype, drought-induced decrease in leaf sucrose concentrations had previously been observed in other legumes (Liu et al. 2004;). According to these reports and others (Scartazza et al. 2001), reduced availability of sucrose has a direct and leading role in limiting the establishment of new sink organs under drought conditions. In the same line, we conclude that drought-induced decrease in the availability of sucrose at source level may have led to a reduced rate of

sucrose export to the sink organs thereby inhibiting reproductive development of the drought-susceptible genotype. On the contrary, we suppose that leaf sucrose accumulation under drought stress for SEA 15 could be due to the inhibition of growth and subsequent decrease in sucrose export to sink organs.

Drought stress caused as much as 63% and 40% reduction in leaf starch concentrations of BrSp and SEA 15, respectively (Fig. 3A). Leaf total non-structural carbohydrate (TNC) (total sugars + starch) concentrations followed same trend (Fig. 3B). Drought-induced decrease of TNC was more pronounced for BrSp (up to 49% reductions) compared with SEA 15, which experienced only up to 26% reduction (Fig. 3B). Relative to the control plants, leaf sucrose to starch ratio increased significantly (except at 20 d) under drought stress for BrSp, whereas the stress did not significantly alter the proportion of the two carbohydrates at all sampling times for SEA 15 (Fig. 4).

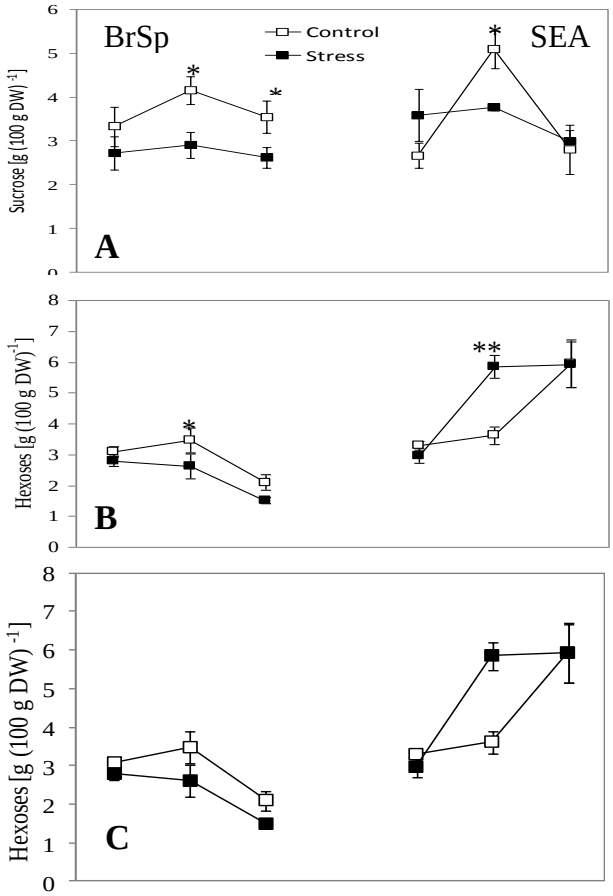

Figure 2. The effect of drought stress imposed at early pod-filling stage on leaf sucrose (A) hexose sugars (B) and total sugars (C) concentrations of two common bean genotypes.

*, ** Indicate significant differences between drought stressed and control treatments at 5 and 1% levels of probability, respectively, according to t-test. Vertical bars are ± S.E. of four replications

A linear relationship of assimilation rate with both starch and sucrose synthesis has been found in common bean leaves, although sucrose is the more preferred product than starch at very low assimilation rates (Sharkey et al. 1985). Drought-induced increase in leaf sucrose to starch ratio found for BrSp (Fig. 4) is consistent with the above report. The modification in carbon partitioning between the two carbohydrates in favor of sucrose could be due to the fact that sucrose is the exclusive form of carbohydrate required for export to the various sink organs for metabolism and storage. Similar findings of increased ratio of leaf sucrose to starch as adaptive feature to different types of stresses including drought (e.g. da Silva and Arrabaça 2004) and cold (e.g. Savitch et al. 2000) have been reported. Modification in carbon partitioning under drought stress (favoring sucrose rather than starch synthesis) during photosynthesis is primarily due to the up-regulation of the enzyme of sucrose synthesis, sucrose phosphate synthase (SPS) (Baxter et al. 2001).

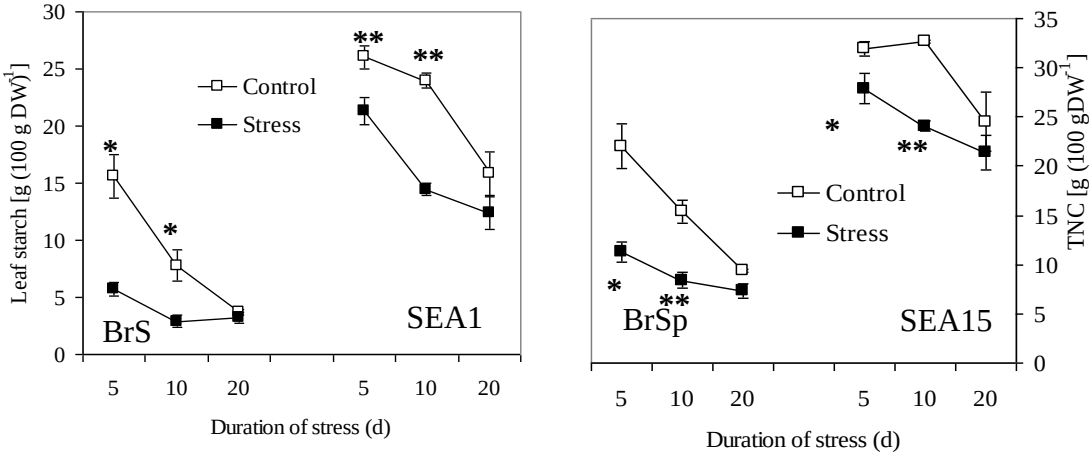

Fig. 3. The effect of drought stress imposed at early pod-filling stage on leaf starch (A) and total non-structural carbohydrate (TNC) (B) concentrations of two common bean genotypes.
*, ** Indicate significant differences between drought stressed and control treatments at 5 and 1% levels of probability, respectively, according to t-test. Vertical bars are ± S.E. of four replications.

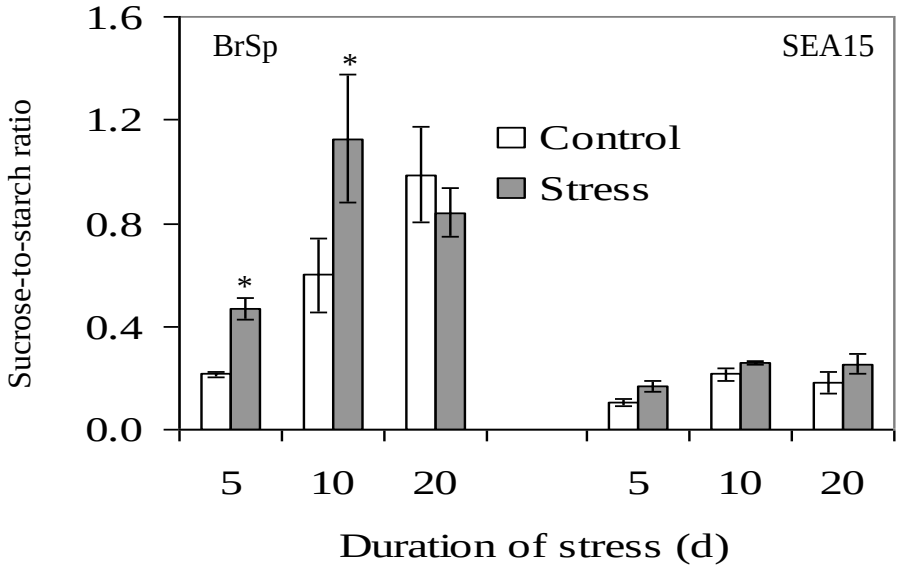

Fig. 4. The effect of drought stress imposed at early pod-filling stage on the ratio of leaf sucrose to starch concentrations of two common bean genotypes.

* Indicate significant differences between drought stressed and control treatments at 5% level of probability, according to t-test. Vertical bars are ± S.E. of four replications. The unit used to calculate the ratio was g (100 g DW)$^{-1}$.

Assimilate import and availability in sink organs

Drought stress did not alter pod sucrose concentrations of the two bean genotypes (Fig. 5A). On the other hand, pod hexose sugar concentration was negatively affected due to drought for BrSp but not for SEA 15 (Fig. 5B). Drought-induced decreases in pod hexose sugar concentrations for BrSp at 5 and 10 d stress were ca. 28 and 30%, respectively (Fig. 5B). Pod total sugar (sucrose + hexose sugars) concentrations for BrSp decreased in response to drought, whilst the concentration remained unaffected for the drought-resistant genotype, SEA 15 (Fig. 5C).

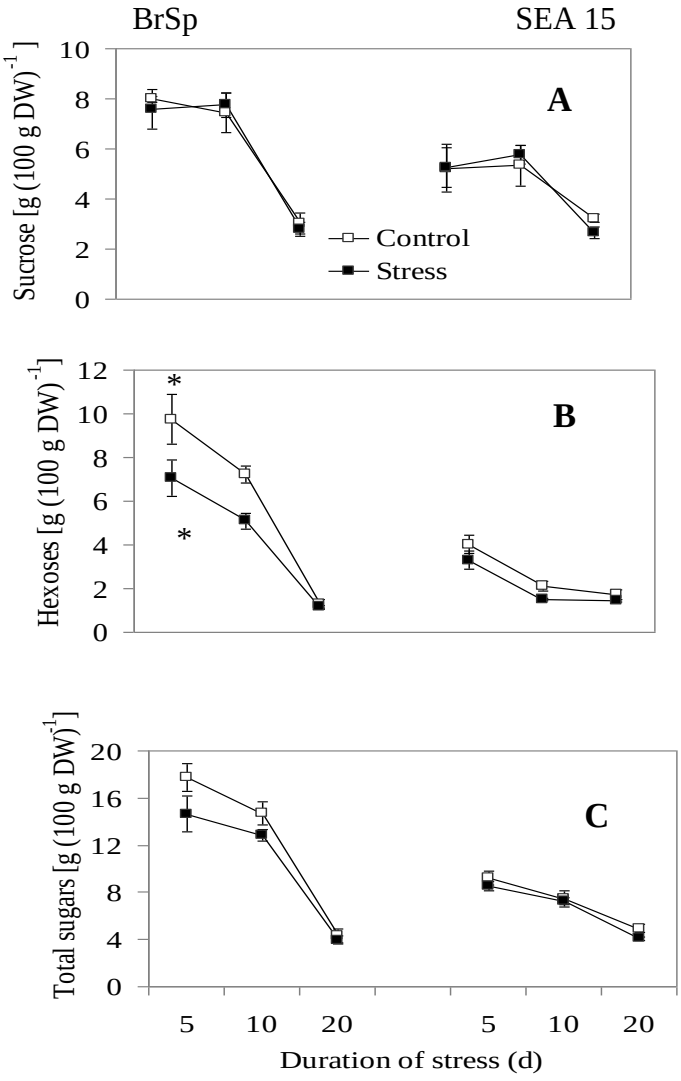

Fig. 5. The effect of drought stress imposed at early pod-filling stage on productive pod sucrose (A), hexose sugars (B) and total sugars (C) concentration of two common bean genotypes.
* Indicate significant differences between drought stressed and control treatments at 5% levels of probability, according to t-test. Vertical bars are ± S.E. of four replications.

Profound genotypic differences were found in terms of the level of sucrose available for metabolism in the seeds under drought stress conditions. In BrSp, drought initiated at early pod-filling stage caused ca. 29% (5 d stress) to 47% (10 d stress) reduction in seed sucrose concentration relative to the non-stressed plants (Fig. 6). On the contrary, seed sucrose concentrations for SEA 15 increased significantly by about 43 (at 10 d stress) and 19% (20 d stress) as a consequence of the stress imposed. Seed

α-amino N concentrations of the genotypes under the contrasting growth conditions were parallel with concentrations found in the leaves and pods. Relative to the control treatments, drought stress significantly increased seed α-amino N concentration by about 12 and 14% for BrSp and SEA 15, respectively (Fig. 7).

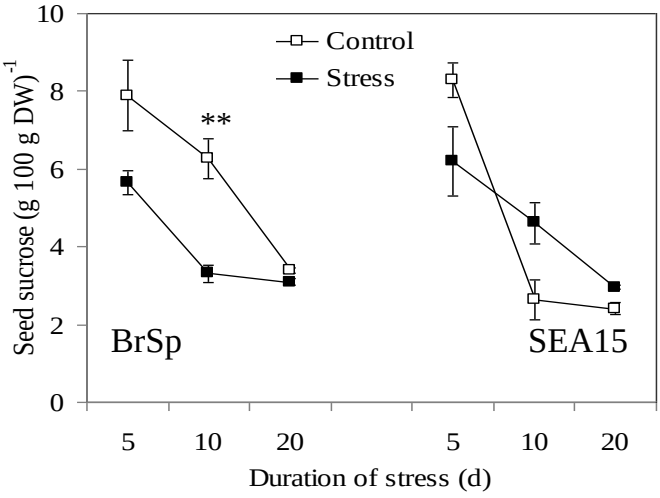

Fig. 6. The effect of drought stress imposed at early pod-filling stage on seed sucrose concentrations of two common bean genotypes.

** Indicate significant differences between drought stressed and control treatments at 1% level of probability, according to t-test. Vertical bars are ± S.E. of four replications.

In the above context, we suppose that in addition to sucrose availability, the capacity for utilizing the assimilate may have been differentially affected in the two bean genotypes under drought stress. The variation in sink strength (ability to metabolize imported sucrose by the pods) may, therefore, partly explain the observed genotypic difference in the establishment and growth of reproductive structures under drought conditions. According to Liu et al. (2004), decreased sucrose utilization in the pods of drought-stressed plants inhibits cell division in young ovules and pod walls leading to higher suppression of growth and eventual abortion of pods.

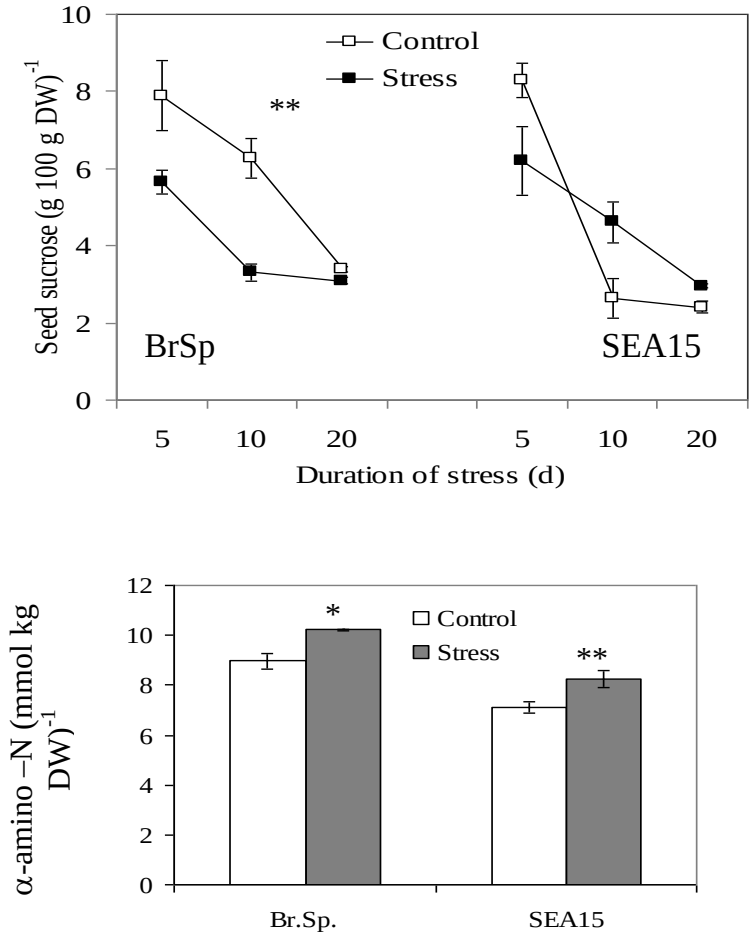

Fig. 7. The effect of drought stress imposed at pod-filling stage on seed α-amino-N concentrations of two common bean genotypes.

*, ** Indicate significant differences between drought stressed and control treatments at 5 and 1% levels of probability, respectively, according to t-test. Vertical bars are ± S.E. of four replications.

Assimilation of storage products in seeds

Although a genotypic difference was evident with regard to the length of the stress period at which the effects began to be manifested, seed starch concentrations of both bean genotypes were decreased under drought stress (Fig. 8). Drought-induced decrease in seed starch accumulation was more consistent across the stress period considered for BrSp than for SEA 15. Plants of BrSp subjected to drought stress for 5 and 20 d had ca. 16 and 18% less seed starch concentrations than the corresponding non-stressed plants, respectively (Fig. 8). For the drought-resistant genotype, SEA 15, drought stress of up to 10 d did not affect seed starch accumulation. However, when the stress period was prolonged to 20 d, seed starch concentration of the genotype decreased by ca. 20% relative to non-stressed plants (Fig. 8). Seed protein

concentrations of neither of the genotypes were affected due to drought stress relative to the corresponding non-stressed treatments (Fig. 9).

Sucrose metabolism is pivotal in seed development and is particularly susceptible to drought stress (Pinheiro et al. 2005). The decrease in seed sucrose concentration due to drought at all durations of stress considered for BrSp (Fig. 6) reflected the lower availability of the assimilate at source level (Fig. 2A). We were not able to show a direct relationship between reproductive sink establishment and photosynthate flux from leaves to pods or seeds. Direct relationship between sucrose availability and export rate at source level and the establishment of new sink organs has been shown for other crops (Liu et al. 2004; Setter et al. 2001). In line with these reports, we suppose that the higher decrease in sink size (number of pods and seeds) of the drought-susceptible genotype due to drought stress is partly attributed to reduced availability of the assimilate at source level (Ho 1988).

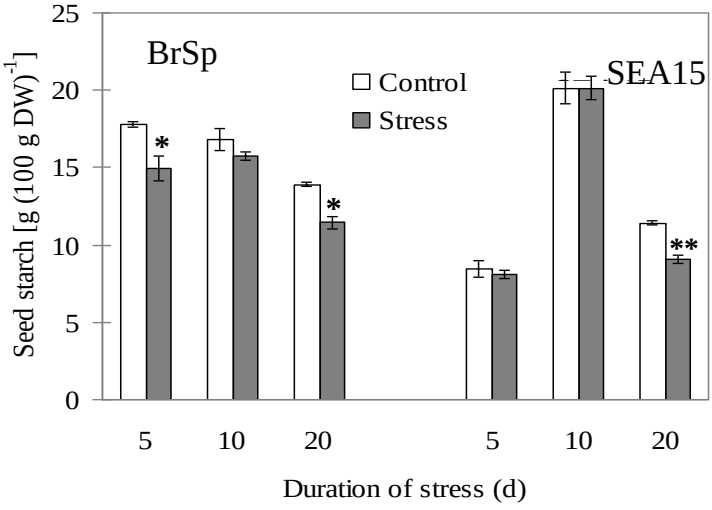

Fig. 8. The effect of drought stress imposed at early pod-filling stage on seed starch concentrations of two common bean genotypes.

*, ** Indicate significant differences between drought stressed and control treatments at 5 and 1% levels of probability, respectively, according to t-test. Vertical bars are ± S.E. of four replications.

The drought-induced decreases in seed starch concentration of BrSp were observed at all harvesting times (5 to 20 d stress) (Fig. 8) corresponding with seed sucrose levels measured during similar periods. In wheat endosperm, Jenner et al. (1991) found a similar relationship between the two seed carbohydrates that the rate of storage starch accumulation was a function of the concentration of sucrose. Based on these relationships, it is appears that shortage of assimilate (sucrose) could be one of the prime factors responsible for the reduced starch accumulation in the seeds of the drought-susceptible bean genotype. On the contrary, reduced seed starch concentration found for SEA 15 (only at 20 d stress) (Fig, 8) was not accompanied by a

decrease in seed sucrose level concurring similar results reported maize (Zinselmeier et al. 1999). These results imply that apart from assimilate availability *per se*, drought stress may induce other factors that contribute to decreased seed starch synthesis. Limitations of sink activities due to the inhibition of the activities of key enzymes of sucrose metabolism (Weber et al. 2005) and starch synthesis (Zinselmeier et al. 1999; Sheoran and Saini 1996; Ho 1988) have been cited as principal factors responsible for reduced starch synthesis under drought situations.

In conclusion, our study demonstrated that the differences in reproductive sink establishment and yield of the bean genotypes under drought conditions are primarily determined by source strength (availability of assimilates in the leaves) rather than by sink attributes.

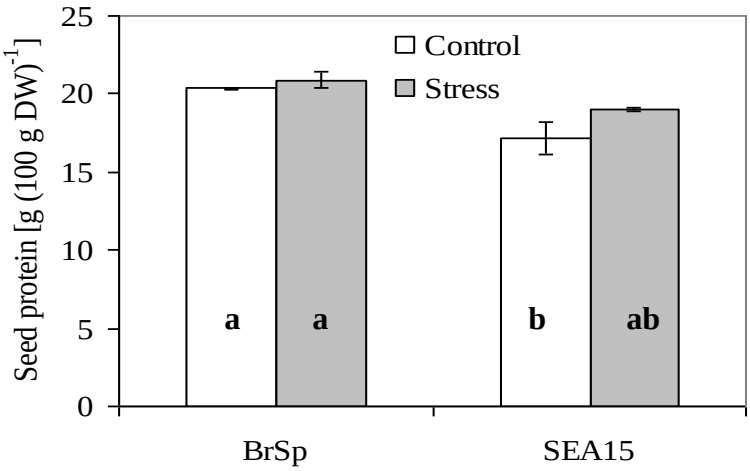

Fig. 9. The effect of drought stress imposed at pod-filling stage on seed protein concentrations of two common bean genotypes.

Means followed by same letter are not significantly different according to LSD test at 5% level of probability. Vertical bars show ±S.E. of four replications.

Acknowledgments

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