Water deficit stress affects photosynthesis and the sugar profile in source and sink tissues of groundnut (*Arachis hypogaea* L.) and impacts kernel quality


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**Summary**

Water deficit stress conditions disturb photosynthetic activity of plants and thereby affect further growth and the mobilization of assimilates towards sink tissues. The influence of mid-season drought on sugar metabolism in both source and sink tissues and its sustained effect on kernel quality across three different habit groups of groundnut was investigated. The experiment was conducted in Kharif 2012 and water deficit stress was created by withholding irrigation for 40 days between 30-70 days after sowing under rain-out shelter to simulate mid-season drought condition. Imposition of water deficit stress reduced net photosynthesis rate, which significantly altered the sugar profiles in leaf. The content of glucose, fructose and sucrose decreased in the leaf tissue, whereas the content of sugar alcohol (inositol and mannitol) and trehalose increased. The sugar profile of the sink tissue (kernel) was also altered under stress but changes were slightly different. The sugar alcohol and oligosaccharides (RFOs) showed significant increase, but the level of mono- and di-saccharides did not show significant change. The results suggested different drought tolerance strategies in source and sink tissues. The kernel quality was also affected under stress with lower oil and higher protein content. The content of oleic acid was reduced, while linoleic acid increased resulting in a decrease of the O/L ratio and oil stability. Alteration of quality traits was least in Spanish genotypes, suggesting a relatively better tolerance of this group for water deficit stress.

**Introduction**

Groundnut is an important oil seed legume grown worldwide mostly in arid and semi-arid region. Over 60% of global groundnut production is crushed for extraction of oil for edible and industrial use, while 40% is consumed in food uses and as seed for sowing the next season crop (BIRTHAL et al., 2010). For the food industries, nutritional composition (oil, protein, fatty acid, amino acids and sugars) of groundnut is equally important with physical and sensory characteristics. The groundnut, mostly grown as rainfed in the arid and semi-arid regions is highly vulnerable to drought stresses of varying duration and intensity due to uncertain rainfall pattern (SINGH et al., 2013). Depending on the time of occurrence, drought has been characterized as early season, mid-season, and end-of-the-season drought. Mid- and end-of-the-season droughts are critical as they affect the pod yield and quality (JANILA et al., 2013). Water deficit stress during pod-development phase is detrimental to several physiological and biochemical processes (NAUTIYAL et al., 1991). Water stress conditions disturb photosynthetic activity of plants and thereby affects further vegetative growth and the mobilization of assimilates towards storage or sink tissues. Sugars in plants, derived from photosynthesis, act as substrates for energy metabolism and the biosynthesis of complex carbohydrates, providing sink tissues with the necessary resources for growth and development. Responses to a specific stress can vary with the genotype, but some general reactions occur in all. Under sugar depleted condition, substantial physiological and biochemical changes occur to maintain respiration and other metabolic processes (JOURNET et al., 1986). Sucrose and glucose either act as the substrates for cellular respiration or as the osmolytes to maintain cellular osmotic potential (GUPTA et al., 2005). Sugars have also been shown to directly protect membranes and proteins in vitro, possibly by replacing water molecules and altering physical properties through the formation of hydrogen bonds (CROWE et al., 1992). The production and partitioning of metabolically important non-structural carbohydrates (starch and sugar alcohols) have been reported to accumulate during drought (KELLER and LUDLOW, 1993). A linear polyhydric alcohol, mannitol, has been reported to increase in response to salt stress mostly due to the osmotic factor of salt stress than its ionic toxicity (PHARR et al., 1995). Expression of the *mitD* gene for the biosynthesis of mannitol improved tolerance to water stress in transgenic groundnut plants (BHAUSO et al., 2014). Another important sugar alcohol which has diverse role in plant biology is myo-inositol, a six carbon cyclohexane hexitol. Myo-inositol is not only required in plant growth and development, but also required as a precursor and substrate for many crucial metabolites in plants such as phytate, phosphatidylinositol, galactinol, raffinose-family oligosaccharides (RFOs), ascorbate, indole acetic acid conjugate, ononitol, and pinitol. These inositol derivatives were shown to be implicated in various physiological and signal processes including plant stress adaptation (LOEWUS and MURTHY, 2000; DONAHUE et al., 2010).

Although, there are a few reports on the effect of drought stress on yield and kernel quality of groundnut (DWIVEDI et al., 1996; CHAKRABORTY et al., 2013), yet adequate information on its impact on sugar profiles of the source and sink tissues and kernel quality is not available. Thus, present investigation was conducted to study the impact of mid-season drought on the sugar profile in source and sink tissues and also consequent effect on kernel quality traits.

**Materials and methods**

**Plant material and growing condition**

An experiment was conducted in Kharif 2012 (June-October) using 12 popular groundnut cultivars, four each from three different habit groups (Spanish bunch type (SB): AK 159, DRG 1, JL 286, TPG 41; Virginia bunch (VB) type: GG 20, HNG 10, ICGS 76, Kadiri 3; Virginia runner (VR) type: GG 11, GG 16, CSMG 84-1, Somnath) at the research farm of the Directorate of Groundnut Research, Junagadh, Gujarat, India. The cultivars were raised in both open field (rain-fed with protective irrigation, unstressed) and rain-out shelter (ROS; imposed water deficit stress). The water deficit stress was imposed by withholding the irrigation after 30 days after sowing (DAS) and continued up to 70 DAS in the ROS. Samples were collected from third upper leaf in triplicate from 70 days old plants. The crop was harvested at full maturity and after curing, the kernel

* Corresponding author
samples were collected from both control and water deficit stressed plots for analysis of quality attributes.

The weather condition during the study period was presented in Tab. 1. Due to imposition of water deficit stress by withholding irrigation for 40 days from 30-70 DAS, soil moisture content was reduced from 18.5% to 10.9% at 0-15 cm soil depth and 19.1% to 12.3% at 15-30 cm soil depth compared to irrigated control plot where optimum moisture level (18.5-19.1%) was maintained throughout the crop growth period (Fig. 1). These values correspond to the threshold value below which groundnut productivity is severely affected. All the cultivars studied started experiencing water deficit conditions at about 45 DAS, some cultivars (DRG 1, Kadiri 3, Somnath) started a few days before.

Measurement of net photosynthesis rate \( (P_N) \)
Net photosynthesis rate \((P_N)\) was measured using a portable photosynthesis system (Model LI-6400, LI-COR, USA) between 09:30-11:30 h local time. Temperature was set at ambient with a stable \( T_{\text{leaf}} \) reading. Photosynthetically active radiation (PAR) was set at 1,650 \( \mu\text{mol}\text{(photon)} \text{ m}^{-2} \text{s}^{-1} \) inside the cuvette, and \( \text{CO}_2 \) was supplied artificially to keep the concentration stable at 400 \( \mu\text{mol} \text{ m}^{-2} \text{s}^{-1} \) inside the chamber (Singh et al., 2014).

Oil and protein content
Oil and protein content of groundnut meal were determined by standard methods i.e. Soxhlet and Kjeldahl method, respectively.

Fatty acid analysis
The fatty acids methyl esters (FAME) of groundnut oil were prepared and analyzed by gas chromatography. In a 10 ml screw cap test tube, 200 \( \mu\text{l} \) oil was mixed with 3 ml hexane and kept for 1 hour at room temperature with intermittent mixing using vortex. After that 3 ml of freshly prepared Sodium methoxide (80 mg NaOH in 100 ml methanol) was added and incubated at room temperature for 30 min. Then 3 ml of 0.8% aqueous sodium chloride was mixed with gentle shaking. Solution was allowed to settle for 5 min and the upper layer of hexane containing the methyl-esters were transferred in screw capped glass vial containing 100 mg anhydrous sodium sulphate (Misra and Mather, 1998). The FAME (10 \( \mu\text{l} \)) of groundnut oil were analysed by Gas Chromatograph (Netel India Ltd., Model MICHRO 9100), using 15% DEGS packed column. The oven temperature during analysis kept at 190 °C, injector temperature at 240 °C and FID detector temperature at 260 °C. Carrier gas (nitrogen) flow rate was maintained at 30 ml min\(^{-1}\) and fuel gas (hydrogen) flow at 30 ml min\(^{-1}\).

Extraction of sugars, free amino acids and total phenolics
The 500 mg of defatted flour was homogenized with 10 ml of 80% ethanol in glass vial and kept in boiling water bath for 10 min. After that, samples were centrifuged at 5000 rpm for 10 min. Extraction was repeated three times with 10 ml of 80% ethanol and supernatants were pooled into 100 ml volumetric flasks and referred as ethanol extract hereafter.

Estimation of free amino acids and total phenolics
The total free amino acids and total phenolics from ethanol extract were determined by using ninhydrin and Folin-Ciocalteu reagents respectively, as described in our earlier reports (Bish et al., 2015). Briefly, for total free amino acid estimation, 0.4 ml of ethanol extract was taken in test tube. A 5 ml of ninhydrin reagent (5:12:2; 1% ninhydrin in 0.5 M citrate buffer pH 5.5: Glycerol: 0.5 M Citrate buffer pH 5.5) was added and mixed thoroughly. The tubes were then placed in a boiling water bath for 12 min and brought to room temperature under running water. The absorbance of the colour was read at 570 nm. The standard curve was prepared by using glycine in the range of 0-80 \( \mu\text{g} \).

For total phenols, one ml of ethanol extract was transferred to a test tube and evaporated till dryness. The residue was dissolved in 1.0 ml water and 0.5 ml of Folin-ciocalteu reagent (1 N), was added to each test tube, mixed, and allowed to stand for 3 min. Subsequently, 2 ml of 20% Na\(_2\)CO\(_3\) was added, mixed thoroughly and then placed in a boiling water bath for one min. After that test tubes were cooled in ice water and the colour was read at 650 nm. Catechol in the range of 0-25 \( \mu\text{g} \) was used as the standard.

Tab. 1: Monthly mean weather data during crop growth period (Kharif 2012). Figures in parenthesis under the field rainfall represent total number of rainy days during that month.

<table>
<thead>
<tr>
<th>Month</th>
<th>Temperature (°C)</th>
<th>Relative humidity (%)</th>
<th>Evaporation (mm)</th>
<th>Rainfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Max</td>
<td>Min</td>
<td>Mean</td>
<td>Max</td>
</tr>
<tr>
<td>June</td>
<td>36.5</td>
<td>27.0</td>
<td>31.7</td>
<td>79</td>
</tr>
<tr>
<td>July</td>
<td>33.7</td>
<td>26.2</td>
<td>30.0</td>
<td>86</td>
</tr>
<tr>
<td>August</td>
<td>32.0</td>
<td>25.0</td>
<td>28.5</td>
<td>91</td>
</tr>
<tr>
<td>September</td>
<td>32.0</td>
<td>24.5</td>
<td>28.2</td>
<td>89</td>
</tr>
<tr>
<td>October</td>
<td>37.0</td>
<td>21.5</td>
<td>29.2</td>
<td>66</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Sugar profiles by ion chromatography
Sugars extracted in ethanol were separated by ion chromatography as reported in our earlier paper (BISHI et al., 2013). Glucose, fructose, myo-inositol, lactose, sucrose, raffinose, stachyose, and verbascose were used as standards. Lactose was used as internal standard during the analysis. The concentrations of various components in the standard mixture were adjusted to such levels that a distinct peak for each was obtained in the chromatogram. Ethanol extracts were membrane-filtered and an aliquot of 25 μl of samples was injected in the ion chromatograph (ICS 3000 Dionex, USA) equipped with amino trap column, CarboPac PA10 guard column followed by CarboPac PA10 analytical column. Sugars were eluted from column in 150 mM NaOH with a flow rate of 1 ml min⁻¹. Data integration was attained by using Chromeleon software supplied with the equipment.

Statistical analysis
All the data recorded were the mean values of at least three independent assays with three replications each. The data was subjected to analysis of variance appropriate to the experimental design. Differences at LSD<sub>P=0.05</sub> were considered statistically significant.

Results
Effect of water deficit stress on photosynthesis
Water deficit stress significantly reduced the rate of photosynthesis in all the genotypes; however there were enough variations observed in the genotypes of different habit group (Fig. 2). In terms of percentage change in net photosynthetic rate Virginia genotypes showed greater reduction compared to Spanish type. At individual genotype level, HNG 10 showed highest reduction (32.7%) in photosynthesis rate followed by Somnath (29.7%) and Kadiri 3 (28.1%). This result suggested, for photosynthetic parameters relatively greater susceptibility of Virginia type peanut cultivars to water deficit stress than Spanish type.

Changes in the sugars profile in the leaf tissue
Imposition of water deficit stress altered the sugar profile in leaf tissues as a result of changes in the net photosynthesis as well as partitioning of the net photosynthate for production of carbohydrates (Tab. 2). Content of both inositol and mannitol increased in the leaf tissue under water deficit stress in all the genotypes across different habit groups. On an average the inositol content almost doubled in Spanish group, whereas the increase in Virginia group was about 50%. Among the genotypes JL 286 and TPG 41 showed highest increase (148 and 125%, respectively) in inositol content under stress compared to the control plants. Similarly, accumulation of mannitol in the leaf tissue also showed the increasing trend under stress. The increase was highest in SB habit group (86%), followed by VR (46%) and VB (33%) group. Among the genotypes, again JL 286 showed highest increase in mannitol accumulation and it increased to 521 ppm under stress from the control value of 245 ppm, whereas genotype ICGS 76 showed least increase (10%).

Tab. 2: Sugar profiles (ppm) of groundnut leaves during water deficit stress

<table>
<thead>
<tr>
<th>Habit Group</th>
<th>Cultivar</th>
<th>Inositol</th>
<th>Mannitol</th>
<th>Trehalose</th>
<th>Glucose</th>
<th>Fructose</th>
<th>Sucrose</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Control</td>
<td>Stress</td>
<td>Control</td>
<td>Stress</td>
<td>Control</td>
<td>Stress</td>
</tr>
<tr>
<td>Spanish Bunch</td>
<td>AK 159</td>
<td>7119</td>
<td>7774</td>
<td>206</td>
<td>435</td>
<td>254</td>
<td>443</td>
</tr>
<tr>
<td></td>
<td>DRG 1</td>
<td>5065</td>
<td>10167</td>
<td>259</td>
<td>357</td>
<td>219</td>
<td>304</td>
</tr>
<tr>
<td></td>
<td>JL 286</td>
<td>4915</td>
<td>12209</td>
<td>245</td>
<td>521</td>
<td>150</td>
<td>643</td>
</tr>
<tr>
<td></td>
<td>TPG 41</td>
<td>5022</td>
<td>11315</td>
<td>211</td>
<td>390</td>
<td>180</td>
<td>569</td>
</tr>
<tr>
<td>Virginia Bunch</td>
<td>GG 20</td>
<td>5492</td>
<td>10970</td>
<td>273</td>
<td>347</td>
<td>260</td>
<td>192</td>
</tr>
<tr>
<td></td>
<td>HNG 10</td>
<td>7629</td>
<td>9694</td>
<td>169</td>
<td>293</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>ICGS 76</td>
<td>6035</td>
<td>9707</td>
<td>281</td>
<td>307</td>
<td>440</td>
<td>402</td>
</tr>
<tr>
<td></td>
<td>Kadiri 3</td>
<td>7724</td>
<td>11869</td>
<td>280</td>
<td>340</td>
<td>13</td>
<td>ND</td>
</tr>
<tr>
<td>Virginia Runner</td>
<td>CSMG 84-1</td>
<td>5169</td>
<td>5884</td>
<td>307</td>
<td>372</td>
<td>369</td>
<td>203</td>
</tr>
<tr>
<td></td>
<td>GG 11</td>
<td>7078</td>
<td>7961</td>
<td>251</td>
<td>393</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>GG 16</td>
<td>6687</td>
<td>8478</td>
<td>316</td>
<td>469</td>
<td>243</td>
<td>154</td>
</tr>
<tr>
<td></td>
<td>Somnath</td>
<td>5507</td>
<td>10296</td>
<td>191</td>
<td>304</td>
<td>119</td>
<td>250</td>
</tr>
<tr>
<td>LSD (P=0.05)</td>
<td>Variety</td>
<td>71.3</td>
<td>14.2</td>
<td>14.4</td>
<td>118.4</td>
<td>130.1</td>
<td>222.9</td>
</tr>
<tr>
<td></td>
<td>Treatment</td>
<td>299.8</td>
<td>NS</td>
<td>27.3</td>
<td>450.5</td>
<td>282.5</td>
<td>78.4</td>
</tr>
<tr>
<td></td>
<td>V × T</td>
<td>100.9</td>
<td>20.1</td>
<td>20.4</td>
<td>167.4</td>
<td>184.1</td>
<td>315.3</td>
</tr>
</tbody>
</table>

ND: not detected, NS: means non-significant
On the other hand, the content of different mono- and disaccharide were reduced with imposition of stress, except trehalose (Tab. 2). Under stress, trehalose content in the leaf showed significant increase mostly in SB genotypes; however for Virginia genotypes it remained either unchanged or even reduced in some cases, except Somnath which showed almost 67% increase. Among the genotypes JL 286 and TPG 41 showed highest increase up to 643 and 569 ppm from a control value of 150 and 180 ppm, respectively. The content of other free sugar viz. glucose, fructose and sucrose reduced in all the genotypes under stress and the highest reduction was observed in SB genotypes (36, 42 and 57% reduction, respectively for glucose, fructose and sucrose), followed by VB and VR group.

**Changes in the sugars profile in the kernel**

Like that of leaf sugar alcohols level, similar increasing trend was also observed in kernel under stress (Tab. 3). The level of inositol was more than doubled in the kernel of Spanish genotypes under stress, whereas the increase was less than half for Virginia genotypes. Among the genotypes JL 286 and TPG 41 showed highest increase (150 and 115% respectively), under stress quite similar to that of leaf tissue. Mannitol content in the kernel also increased significantly under stress and among different habit groups SB showed highest increase, followed by VR and VB group. The genotype JL 286 again showed highest increase mannitol content (144%), while least increase was observed for HNG 10 (14%).

Trehalose content in the kernel was increased under stress only in SB group, and it was significantly reduced in both VB and VR group (Tab. 3). Highest increase in trehalose content was observed in JL 286 (103%), followed by TPG 41 (69%), while the genotype CSMG 84-1 showed highest reduction (69%). The glucose content in the kernel was increased under stress in almost all the genotypes (84%) in RFOs content under stress, whereas it was 31 and 16% for VR and VB group respectively. Among the genotypes TPG 41 showed highest increase (84%) in RFOs content under stress, followed by JL 286 (47%), while the genotypes ICGS 76 and CSMG 84-1 showed least change in RFOs content when the stress was imposed.

**Changes in kernel quality parameters**

Imposition of water deficit stress significantly reduced the oil yield and altered different kernel quality parameters in all the genotypes (Tab. 4). Among different habit groups, SB showed least loss in oil content, where highest oil loss was observed in VR group. Among the genotypes JL 286 showed the least reduction (1.8%) in oil content whereas Somnath showed the highest reduction (13.1%). Unlike oil the total protein content increased under stress, the genotype CSMG 84-1 showed highest increase (23.4%), followed by JL 286 (22.7%). The free amino acid content was also increased under stress and the highest increase was observed in CSMG 84-1, where increased up to 4.30 mg g⁻¹ seed weight from a control value of 2.23. This increase in free amino acid content might possibly be due to increase in kernel protein content as well as stress induced breakdown of it. The total phenol content showed a mixed response under stress. Although the varietal differences were significant, but no significant treatment effect was observed in the present study.

**Changes in oil quality parameters**

Imposition of water deficit stress altered the relative content of oleic and linoleic acid in the groundnut kernel, ultimately altering the O/L ratio and the keeping quality of the oil (Fig. 3). Oleic acid content

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**Tab. 3:** Sugar profiles (ppm) of groundnut kernels during water deficit stress

<table>
<thead>
<tr>
<th>Habit Group</th>
<th>Cultivar</th>
<th>Inositol</th>
<th>Mannitol</th>
<th>Trehalose</th>
<th>Glucose</th>
<th>Sucrose</th>
<th>RFOs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Span. Bunch</td>
<td>AK 159</td>
<td>464</td>
<td>826</td>
<td>207</td>
<td>387</td>
<td>601</td>
<td>894</td>
</tr>
<tr>
<td></td>
<td>DRG 1</td>
<td>517</td>
<td>910</td>
<td>290</td>
<td>575</td>
<td>311</td>
<td>489</td>
</tr>
<tr>
<td></td>
<td>JL 286</td>
<td>320</td>
<td>807</td>
<td>300</td>
<td>731</td>
<td>751</td>
<td>1524</td>
</tr>
<tr>
<td></td>
<td>TPG 41</td>
<td>512</td>
<td>1094</td>
<td>577</td>
<td>1026</td>
<td>74</td>
<td>124</td>
</tr>
<tr>
<td>Virginia Bunch</td>
<td>HNG 10</td>
<td>700</td>
<td>840</td>
<td>553</td>
<td>635</td>
<td>50</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>ICGS 76</td>
<td>694</td>
<td>911</td>
<td>505</td>
<td>703</td>
<td>211</td>
<td>103</td>
</tr>
<tr>
<td></td>
<td>Kadiri 3</td>
<td>670</td>
<td>892</td>
<td>611</td>
<td>930</td>
<td>57</td>
<td>67</td>
</tr>
<tr>
<td>Virginia Runner</td>
<td>CSMG 84-1</td>
<td>996</td>
<td>1429</td>
<td>473</td>
<td>835</td>
<td>579</td>
<td>178</td>
</tr>
<tr>
<td></td>
<td>GG 11</td>
<td>545</td>
<td>739</td>
<td>760</td>
<td>995</td>
<td>449</td>
<td>254</td>
</tr>
<tr>
<td></td>
<td>GG 16</td>
<td>1093</td>
<td>1246</td>
<td>459</td>
<td>601</td>
<td>234</td>
<td>198</td>
</tr>
<tr>
<td></td>
<td>Somnath</td>
<td>347</td>
<td>579</td>
<td>660</td>
<td>936</td>
<td>313</td>
<td>127</td>
</tr>
</tbody>
</table>

| LSD (P=0.05) | Variety (V) | 31.6  | 39.6  | 52.3  | 5.1   | 198.1  | 67.7 |
|              | Treatment (T)| 33.7  | 10.6  | NS    | NS    | 548.4  | 105.1|
|              | V × T         | 44.7  | 55.9  | 74.1  | 7.1   | 280.1  | 95.8|

ND: not detected, NS: means non-significant
significantly reduced in all the cultivars under water deficit stress (Fig. 3A) however, highest reduction observed in Virginia genotypes than that of Spanish ones. The genotype Kadiri 3 showed the highest reduction (12.9%) in oleic acid content under stress, followed by HNG 10 (11.3%). Linoleic acid content showed the opposite trend and was found to be increased under stress (Fig. 3B). The increase was highest in HNG 10 (31.4%), followed by Kadiri 3 (28.2%), whereas AK 159 showed least change (4.5%) under stress. With the decrease in oleic acid content and concomitant rise in linoleic acid fraction resulted in an obvious decrease in O/L ratio in the groundnut kernels in all the genotypes in the present study (Fig. 3C). The genotypes HNG 10 and Kadiri 3 showed highest reduction in O/L ratio, which was 32.4 and 32.0%, respectively under water deficit stress.

### Discussion

In the present study imposition of prolonged water deficit stress led to significant alternation of physiological and metabolic activities in both source (leaf) and sink (kernel) tissue in groundnut, however the impact varies across different habit groups. Although groundnut is a moderately drought tolerant crop, the imposition of drought stress especially during mid or late season of crop growth significantly reduces various metabolic activities of the crop mainly due to lack of adequate water supply to the active tissue and eventual closure of stomata (Dev et al., 2009). Kalariya et al. (2013) also reported a 11-30% reduction in net photosynthesis in groundnut during water deficit stress. Limitation of photosynthetic activity under severe water deficit stress was also attributed to rapid degradation of thylakoid membranes in groundnut apart from stomatal constraint (Lauriano et al., 2000). A decreased rate of photosynthesis in water deficit stress affects carbon delivery from source to sink tissue and its subsequent metabolism. The photosynthetic rate of leaves decreases as relative water content and water potential decreases. A reduction of the net photosynthetic rate in moisture stressed plants mainly happens through stomatal closure as a mechanism to reduce total transpiration (Singh, 2004; Rosas-Anderson et al., 2014). As a result of reduced photosynthetic activities under water de-
Water deficit stress alters sugar profile in groundnut

Deficit stress, significant alteration in the sugar profile was observed in different groups of groundnut cultivars. Due to lower supply of net assimilate, the carbon partitioning in the leaf tissue changed significantly. The content of readily available carbohydrates (glucose, sucrose and fructose) dropped, whereas carbohydrates necessary for stress tolerance (inositol, mannitol and trehalose) increased upon imposition of stress. Similar increase in the levels of sugar alcohol, particularly the pinitol, and decrease in the levels of sucrose was observed by Keller and Ludlow (1993) in the leaves of pigeon pea after imposition of drought stress. Morsy et al., (2007) reported higher accumulation of osmo-proteoctants like trehalose, inositol and mannitol in the more salt and water-deficit tolerant rice genotype, which suggested role of these organic solutes in osmo-tolerance mechanism in plants. Mannitol, an important photoassimilate which participates in a wide range of physiological processes including carbon storage and translocation, regulation of the pool of the cellular reductant in plants (Stoop and Moolbroek, 1998), scavenging of hydroxyl radicals and serving as an osmotically active compatible solute (Popp and Smirnoff, 1995). In the presents study, increase in the content of inositol, mannitol and trehalose occurs at the expense of simpler carbohydrates such as glucose, fructose and sucrose content in the leaves of stressed plants.

Like the sugar alcohols, trehalose is also proposed as an osmoprotectant during periods of drought or water-deficit stresses (Pennan, 2003). This sugar possesses the unique capacity for reversible water absorption, and appears to be superior to other sugars in protecting biological molecules from desiccation-induced damage (Rontelin et al., 2002). Adverse conditions such as heat, chilling or water stress correlate with the accumulation of high concentrations of trehalose in yeast (Goddin and Van Dun, 1999) and highly desiccation-tolerant resurrection plants (Iturriaga et al., 2000). Differential responses of cultivars from different habit groups to water deficit stress implied their variable ability to tolerate stress. In the present study, Spanish group of cultivars showed highest induction in accumulation of organic solute in response to external water deficit condition suggesting their superior ability to tolerate drought stress than Virginia group of cultivars. Reduction of sucrose content in the leaf tissue during stress condition may contribute to either higher transport towards kernels or its rapid conversion to more complex sugars for better osmo-protection. Thus results from the present study suggest decrease of hexoses under stress condition is likely to be utilized in the biosynthesis of higher sucrose content in the sink tissues. In general, sucrose levels of stressed ovaries are higher or at least similar to those of non-stressed ovaries as reported in maize (Schussler and Westgate, 1995; Zinselmeier et al., 1995).

Although the sugar profile of the kernel (sink tissue) changed significantly like that of leaf (source tissue), the pattern of change was found somewhat different in the present study. Similar to the changes in leaf tissue, the content of sugar alcohols increased along with increase in stress induced oligosaccharide (Raffinose and Stachyose) content, but the level of monosaccharide and disaccharides did not change in stress induced oligosaccharide (Raffinose and Stachyose) concentration. The lack of adequate C-supply from the source tissue (both due to reduced photosynthesis and conversion of assimilate for biosynthesis of organic osmo-protectants) resulted in reduction in kernel oil content, but a relative increase in protein content in the present study. Similarly, Conkerton et al. (1989) also reported that mid-season drought reduced total oil content in groundnut. Oil has negative correlation with protein content thus decrease in oil content may eventually results in increased protein content. However, we do differ from some of the previous reports that total oil and total protein were not significantly affected by mid-season drought (Dwivedi et al., 1996).

Under drought stress, due to shortening of pod development and seed filling period alteration of oil/protein ratio in legume seeds were reported, which was mainly because of the fact that during seed filling accumulation of carbohydrate and protein were much faster than that of oil (Dornbos and Mcdonald, 1986; Kambiranda et al., 2011). Hashim et al. (1993) also observed comparatively higher percentage of linoleic acid (18:2) and lower percentage of oleic acid (18:1) in the groundnut kernels when it was grown under water deficit condition. Our results also suggest that there is a shift of oleic to linoleic acid under water deficit stress resulting in reduced O/L ratio and oil stability.

In conclusion, mid-season water deficit stress in groundnut significantly affects the carbohydrate composition and source and sink sugar profiles. The increase in relative proportions of stress induced complex sugars (myo-inositol and mannitol) in the leaf tissue showing the adaptive response to osmo-tolerance. On the contrary, reduction in simple sugars under stress in the leaf with subsequent translocation to sink tissue suggests a drought escape mechanism in groundnut. Oleic acid content, a measure of oil stability and quality, was also decreased due to water deficit condition. The quality traits were comparatively less affected in Spanish genotypes than in Virginia genotypes due to water deficit stress; hence the Spanish cultivars would be a better choice for the farmers in rain-fed groundnut growing areas.

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References


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