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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 uses, 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 sustain 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 *mtlD* 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

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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.

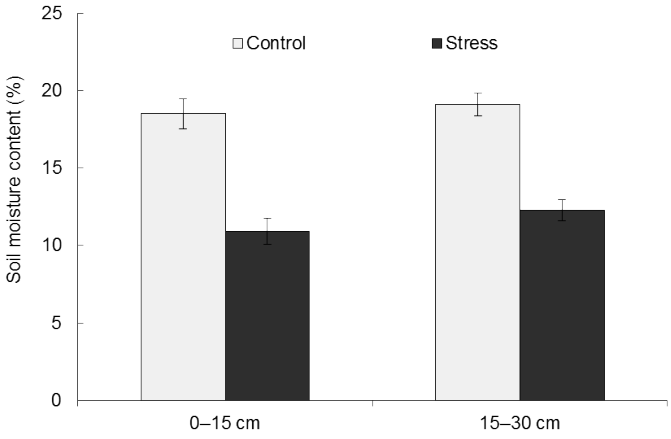

Fig. 1: Changes in soil moisture content (w/w) at different soil depth due to imposition of water deficit stress

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_{leaf} reading. Photosynthetically active radiation (PAR) was set at 1,650 $\mu mol_{(photon)}$ m^{-2} s^{-1} inside the cuvette, and CO_2 was supplied artificially to keep the concentration stable at 400 μmol m^{-2} 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 µl oil was mixed with 3 ml hexane and kept for 1 h 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 MATHUR, 1998). The FAME (10 µl) 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 (BISHI 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 pH5.5: 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 µg.

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_2CO_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 µg 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.

Month	Temperature (°C)			Relative humidity (%)			Evaporation (mm)	Rainfall (mm)
	Max	Min	Mean	Max	Min	Mean		
June	36.5	27.0	31.7	79	50	64	234.0	84.2 (3)
July	33.7	26.2	30.0	86	64	75	139.5	67.6 (6)
August	32.0	25.0	28.5	91	69	80	105.4	79.5 (7)
September	32.0	24.5	28.2	89	67	78	102.0	193.7 (10)
October	37.0	21.5	29.2	66	30	48	186.0	0.0 (0)
Total							766.9	425.0 (26)

Sugar profiles by ion chromatography

Sugars extracted in ethanol were separated by ion chromatograhy 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 $LSD_{P=0.05}$ 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.

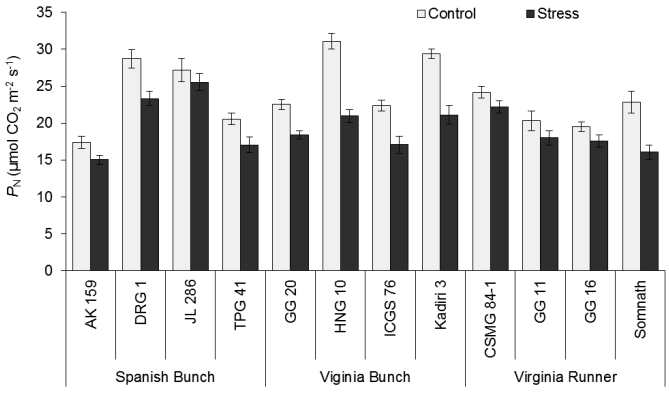

Fig. 2: Changes in net photosynthesis rate (P_N) in groundnut leaves under water deficit stress

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

Habit Group	Cultivar	Inositol		Mannitol		Trehalose		Glucose		Fructose		Sucrose	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress	Control	Stress	Control	Stress
Spanish Bunch	**AK 159**	7119	7774	206	435	254	443	19613	13719	14416	10106	19926	8110
	DRG 1	5065	10167	259	357	219	304	12103	6214	10248	4602	11914	3779
	JL 286	4915	12209	245	521	150	643	10732	8386	9296	6143	16699	5931
	TPG 41	5022	11315	211	390	180	569	19593	11105	16662	8406	20607	13498
Viginia Bunch	**GG 20**	5492	10970	273	347	260	192	14418	11777	9446	8987	21165	9445
	HNG 10	7629	9694	169	293	ND	ND	14198	7853	10574	5746	21284	11203
	ICGS 76	6035	9707	281	307	440	402	13406	9070	11657	7249	22417	15442
	Kadiri 3	7724	11869	280	340	13	ND	13453	9536	10264	7087	20339	13406
Virginia Runner	**CSMG 84-1**	5169	5884	307	372	369	203	9748	7411	7056	5767	12558	7586
	GG 11	7078	7961	251	393	ND	ND	13689	7049	10265	5839	22593	11293
	GG 16	6687	8478	316	469	243	154	10885	10694	8196	8072	18435	2263
	Somnath	5507	10296	191	304	119	250	13273	11490	9582	9090	17438	13692
LSD (P=0.05)	**Variety (V)**	71.3		14.2		14.4		118.4		130.1		222.9	
	Treatment (T)	299.8		NS		27.3		450.5		282.5		78.4	
	V × T	100.9		20.1		20.4		167.4		184.1		315.3	

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, but 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 except GG 11 and GG 16 (Tab. 3). More than 75% increase in kernel glucose content was observed in TPG 41 and Somnath under stress, while in some of the genotypes like Kadiri 3 and CSMG 84-1, the increase was as low as 20%. Unlike that of leaf, the sucrose content in the kernel increased under stress in most of the genotypes except AK 159 and JL 286 (Tab. 3). Highest increase in kernel sucrose content was observed in Somnath, followed by GG 11, where it was increased up to 47.6 and 65.3 mg g^{-1} seed weight under stress from the control value of 27.9 and 47.1mg g^{-1} seed weight, respectively.

Total raffinose family oligosaccharides (RFOs) content (raffinose and stachyose) was also increased in the kernel under stress (Tab. 3). On an average the SB group showed 39% increase 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

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

Habit Group	Cultivar	Inositol		Mannitol		Trehalose		Glucose		Sucrose		RFOs	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress	Control	Stress	Control	Stress
Spanish Bunch	AK 159	464	826	207	387	601	894	86	124	26768	22061	1614	1855
	DRG 1	517	910	290	575	311	489	ND	120	22626	30043	1273	1403
	JL 286	320	807	300	731	751	1524	69	99	40704	34354	1867	2749
	TPG 41	512	1094	577	1026	74	124	170	299	31925	40505	1440	2650
Viginia Bunch	GG 20	368	698	368	424	292	110	ND	71	36569	50318	3341	4088
	HNG 10	700	840	553	635	50	64	83	140	53065	73576	4111	5155
	ICGS 76	694	911	505	703	211	103	ND	172	54806	57069	3667	3668
	Kadiri 3	670	892	611	930	57	67	158	191	45567	63218	4178	4810
Virginia Runner	CSMG 84-1	996	1429	473	835	579	178	104	126	47063	65350	3777	3540
	GG 11	545	739	760	995	449	254	99	ND	35931	50344	2643	3863
	GG 16	1093	1246	459	601	234	198	111	ND	51852	63565	2253	3200
	Somnath	347	579	660	936	313	127	78	139	27888	47652	2251	3167
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

Tab. 4: Effect of water deficit stress on oil, protein, free amino acids and total phenol content of groundnut kernels

Habit Group	Cultivar	Oil (%)		Protein (%)		Free amino acids (mg^{-1} g)		Total Phenol (mg^{-1} g)	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress
Spanish Bunch	AK 159	54.50	53.30	20.60	21.75	2.09	1.82	4.96	4.44
	DRG 1	53.10	51.90	23.50	26.05	2.55	2.85	4.55	4.95
	JL 286	48.05	47.20	30.40	32.90	2.38	2.63	4.21	4.27
	TPG 41	49.75	46.40	24.25	29.75	2.90	2.73	5.25	5.05
Viginia Bunch	GG 20	52.15	48.00	25.70	30.20	2.95	3.80	4.87	5.90
	HNG 10	45.85	43.75	33.75	35.25	2.95	4.28	5.41	5.13
	ICGS 76	48.75	46.95	30.60	32.60	3.02	3.89	5.53	7.05
	Kadiri 3	46.05	43.90	33.05	35.80	3.39	5.04	7.04	6.84
Virginia Runner	CSMG 84-1	48.80	45.15	27.50	33.95	2.23	4.30	4.07	5.83
	GG 11	51.65	45.55	26.55	31.70	2.83	3.85	5.15	5.82
	GG 16	46.30	45.25	32.90	34.50	4.13	5.63	5.22	6.52
	Somnath	53.20	46.25	23.15	32.65	2.41	3.69	4.77	5.00
LSD (P=0.05)	Variety (V)	0.81		1.05		0.13		0.27	
	Treatment (T)	1.98		0.74		0.64		NS	
	V × T	1.16		1.48		0.19		NS	

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 (Devi 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 wa-ter 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-

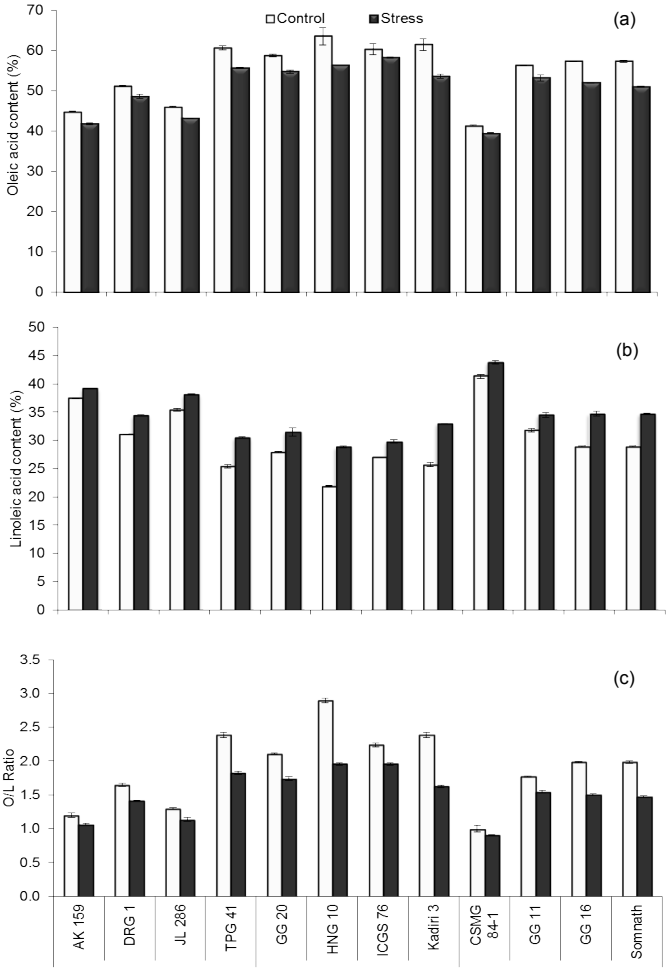

Fig. 3: Changes in Oleic (a), Linoleic (b) acid content and O/L ratio (c) in groundnut cultivars under water deficit stress

ficit 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-protectants 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 MOOIBROEK, 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 (PENNA, 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 (RONTEIN et al., 2002). Adverse conditions such as heat, chilling or water stress correlate with the accumulation of high concentrations of trehalose in yeast (GODDJIN 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 show significant alteration in the kernel tissue. Inositol and its derivatives are implicated in stress tolerance through various ways such as protecting cellular structures from reactive oxygen species, controlling turgor pressure or by acting as stress signaling molecules (LOEWUS and MURTHY, 2000). As non-reducing carbohydrates, RFOs are good storage compounds, being able to accumulate in large quantities without affecting primary metabolic processes. Few previous studies reported that desiccation tolerance is strongly correlated with accumulation of RFOs, primarily raffinose, stachyose, and verbascose in the seeds (HORBOWICZ and OBENDORF, 1994; LIN and HUANG, 1994).

Water deficit stress has dual impact on the end product synthesis in groundnut kernels. Being primarily an oilseed crop, water deficit stress significantly reduced oil yield and thus altered kernel composition. 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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