

# **Recent Advances in CROP PHYSIOLOGY**

**– Volume 1 –**

— Editor —

**Dr. Amrit Lal Singh**

*Principal Scientist,*

*Plant Physiology*

*Directorate of Groundnut Research,*

*Junagadh, Gujarat*

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81, Darya Ganj, Near Hindi Park,

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New Delhi - 110 002

Phone: 011-4354 9197, 2327 8134

Fax: +91-11-2324 3060

E-mail: [info@astralint.com](mailto:info@astralint.com)

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# Chapter 1

## **Physiology of Groundnut under Water Deficit Stress**

*A.L. Singh, Nisha Goswami, R.N. Nakar,  
K.A. Kalariya and K. Chakraborty*

*Directorate of Groundnut Research, P.B. 5, Junagadh – 362 001, Gujarat  
E-mail: [alsingh@nrcg.res.in](mailto:alsingh@nrcg.res.in), [alsingh16@gmail.com](mailto:alsingh16@gmail.com)*

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## **Abbreviations**

- ABA: Abscisic Acid  
ACP: Acid Phosphatase  
ADH: Alcohol Dehydrogenase  
AE: PE: Actual Evapotranspiration: Potential Evapotranspiration  
AP: Apparent leaf photosynthetic rate  
AsA: Ascorbic Acid  
ASM: Available Soil Moisture  
CaM: Calmodulin  
CAT: Catalase  
CATD: Canopy temperatures relative to Air  
CCC: Chlormequat  
CER: Carbon Dioxide Exchange Rate  
CGR: Crop Growth Rates  
CID: Carbon Isotope Discrimination  
CMI: Cell Membrane Integrity  
CMS: Cell Membrane Stability  
CPE: Cumulative Pan Evaporation  
CWSI: Crop Water Stress Index  
DAE: Days after Emergence  
DAP: Days after Planting  
DAS: Days after Sowing  
DD-RT-PCR: Differential Display Reverse Transcription-Polymerase Chain Reaction  
DM: Dry Matter  
DPD: diffusion pressure deficit  
DR: Diffusive Resistance

- DREB: Dehydration Responsive Element Binding
- DS: Drought Stressed
- EFV: Extraction Front Velocity
- EMS: Early Moisture Stress
- ESD: End Season Drought
- EST: Esterase
- EST: Expressed Sequence Tag
- ET/Et: Evapotranspiration
- EWL: Epicuticular Wax Load
- FC: Field Capacity
- FDPP: Fully Developed Pods Plant
- FDPR: Fully Developed Pod Ratio
- FW: Fresh Weight
- FYM: Farm Yard Manure
- GCA: General Combining Ability
- GM: Genetically Modified
- HI: Harvest Index
- IW:CPE: Irrigation Water: Cumulative Pan Evaporation Ratios
- Kc: Crop Coefficients
- ky: Yield Response Factors
- LA: Leaf Area
- LAI: Leaf Area Index
- LE: Latent Heat Flux
- IPAR: Intercepted Photosynthetic Photon Flux Density or Photosynthetically Active Radiation
- IUE: Irrigation-use efficiencies
- LEA: Late Embryogenesis-Abundant
- LER: Land Equivalent Ratio
- LIR: Light Interception Rate
- LWUER: Land water-use equivalency ratio
- LWP: Leaf Water Potential
- MC: Moisture Content
- MDA: Maloni dialdehyde
- MDH: Malate Dehydrogenase
- MLT: Multi-Location Trial
- MSD: Mid-Season Drought
- NDVI: Normalized Difference Vegetation Index

- NRA : Nitrate Reductase Activity  
O:L ratio : Oleic : Linoleic Ratio  
PAR: Photosynthetically Active Radiation  
PF : Partitioning Factor  
PDB: Pee Dee Belemnite  
PEG : Polyethylene Glycol  
PGR: Pod Growth Rate  
PMA: Phenylmercury Acetate  
POD: Peroxidase  
PP 333 : Paclobutrazol  
PWR: Pod:Shoot Wt. Ratio  
QTL: Quantitative Trait Loci  
R/S ratio : Root/Shoot Ratio  
RDF: Recommended dose of Fertilizer  
RILs: Recombinant Inbred Lines  
RLD: Root Length Density  
RPMP: Relative Plasma Membrane Permeability  
RSD: Relative Saturation Deficit  
RSW: Reduced Soil Water Supply  
Rubisco: Ribulose-1, 5-bisphosphate carboxylase-oxygenase  
RUE: Radiation Use Efficiency  
RWC: Relative Water Content  
SAVI: Soil Adjusted Vegetation Index  
SC: Stomatal Conductance  
SCA: Specific Combining Ability  
SCMR: SPAD Chlorophyll Meter Readings  
SD: Saturation Deficit  
SDD: Stress Degree Days  
SLA: Specific Leaf Area  
SMK: Sound Mature Kernels  
SMS: Soil Moisture Stress  
SMT: Soil Moisture Tensions  
SMW: Standard Meteorological Week  
SOD: Superoxide Dismutase  
SOP: Sulphate of Potash  
MOP: Muriate of Potash  
SPAD: Soil Plant Analytical Development

- SPI: Standardized Precipitation Index  
SRWC: Soil Relative Water Content  
SSR: Simple Sequence Repeat  
T: Transpired Water  
 $T_b$ : Base Temperature  
TCPR: Total Crop Performance Ratio  
TE: Transpiration Efficiency  
TLWUER: Total Land Water Use Equivalency Ratio  
TP: Turgor Potential  
TSWV: Tomato Spotted Wilt Virus  
TWP: Temporary Wilting Point  
 $V_a$ : Apparent Sap Velocity  
VPD: Vapour Pressure Deficit  
VPD<sub>la</sub>: Leaf to Air Vapour Pressure Deficit  
WCU: Water Consumptive Use  
 $W_D$ : Water Deficit  
WRC: Water Retention Capacity  
WRSI: Water Requirement Satisfaction Index  
WSD: Water Saturation Deficit  
WT: Wild Type  
WU: Water Use  
WUE: Water Use Efficiency  
WUEc: Water Use Efficiency Corrected  
WW: Well watered

## 1. Introduction

The groundnut (*Arachis hypogaea* L), though native of South America, due to its wide adaptability the cultivation of this important food legume crop has been spread on almost all soils in the tropical and subtropical countries and now grown in about 128 countries in different agro-climatic zones mainly in semi-arid regions between latitudes 40°S and 40°N. However, its cultivation is settled in southern, eastern and south-eastern part of Asia, western Africa and northern and south America owing to favorable soil and climate and presently it is cultivated on 11.5 m ha land in Asian, 11.5 m ha in African and 1.1 m ha in American countries. Groundnut requires warm growing season with well distributed rainfall in the range of 500-1000 mm and on large scale it is mainly grown in semi-arid and arid regions of India, China, Nigeria, USA, Myanmar, Indonesia, Sudan, Senegal, Argentina and Vietnam, Ghana, Chad, Congo Republic, Mali, Guinea, Niger, Argentina, Brazil, Tanzania, Burkino Faso,

and Malawi. More than 85 per cent of the world groundnut production come from food deficit countries with an average productivity of about 1500 kg ha<sup>-1</sup> and having more than 90 per cent of the groundnut growing areas of the world.

The drought is regarded as the most damaging abiotic stress, in sustainable crop production. Groundnut is grown under a wide range of environments where frequent drought is one of the limiting factors adversely affecting its productivity in rainfed area. Groundnut production, fluctuates considerably as a result of rainfall variability, due to its underground fruiting habit and low moisture availability during drought. There is wide range of groundnut productivity varying from about 500 kg ha<sup>-1</sup> (poor) in Angola and Mozambique (extremely low about 300 kg ha<sup>-1</sup>), Madagascar, Namibia, Niger, Uruguay and Zimbabwe, about 3000 kg ha<sup>-1</sup> (high) in China, Egypt, Syrian Arab Republic, about 4000 in USA, Malaysia, Saudi Arabia, Palestine and Nicaragua, as much as 6400 kg ha<sup>-1</sup> (very high) in Israel and extremely high (> 12000 kg ha<sup>-1</sup>) in Cyprus (FAO, 2012). However, the world average yield is around 1600 kg ha<sup>-1</sup> and about 70 per cent of the world groundnut production occurs in the semi-arid to arid tropics where the average yield is still around 1000 kg ha<sup>-1</sup>.

Presently, India has the largest groundnut area of about 6 million hectare (24 per cent of the world), producing about 8 million tonne (mt) of pod accounting for only 20 per cent of the world groundnut production, but China with only 18 per cent area contributes 39 per cent of the world production due to better drought and nutrient management practices. Though the average groundnut yield in India is around 1400 kg ha<sup>-1</sup>, combination of improved genotypes and best agronomic practices recorded more than 6000 kg ha<sup>-1</sup> pod yield frequently and occasionally upto 8000 kg ha<sup>-1</sup> indicating that there is tremendous scope to increase the yield through understanding its physiology and water relation (Singh 2004, 2011; Singh *et al.*, 2013).

Drought, considered to be the most complex but least understood of all natural hazards, is an insidious hazard of nature and large historical datasets are required to study these involving complex interrelationships between climatological and meteorological data. Rainfall is an important meteorological parameter, the amount and distribution influence the type of vegetation in a region. Characterization of agricultural drought is essential before undertaking a yield improvement programme in any crop and a simplified model combining ET and water balance concepts with basic data on plant responses to drought is applicable for diagnosing drought types in groundnut. Accordingly the physiological studies and drought tolerance of this crop started in 1980s and by now ample of studies have been conducted. However, due to underground fruiting, indeterminate growth habit and different botanical types still certain aspects of physiology of this crop, especially moisture requirement of pod zone are not very clear. The research is towards the improvement of the performance of the crop and genotypes under varying degrees of stress at various physiological stages of crop growth.

The introduction of an improved genotypes into new region is largely determined by the temperature and phenology and knowledge of crop physiology under water-deficit stress is important for achieving optimal yield under limited water availability and can be used to specify the most appropriate rate and time of specific developmental



process to maximize yield. In this chapter an attempt was made to synthesize the impact of water deficit stress on the various component of groundnut physiology and management practices to grow high yielding varieties to increase the productivity.

## **2. Defining the Drought Stress and various Parameters**

There is no universally accepted definition of drought, it is a meteorological term and commonly defined as a period without significant rainfall denoting scarcity of water in a region. The irrigation commission of India defines drought as a situation occurring in any area where the annual rainfall is less than 75 per cent of normal rainfall. Prolonged deficiencies of soil moisture adversely affect crop growth indicating incidence of agricultural drought. It is the result of imbalance between soil moisture and evapo-transpiration needs of an area over a fairly long period so as to cause damage to standing crops and to reduce the yields.

### **2.1 Soil Type, Climate and Rainfall**

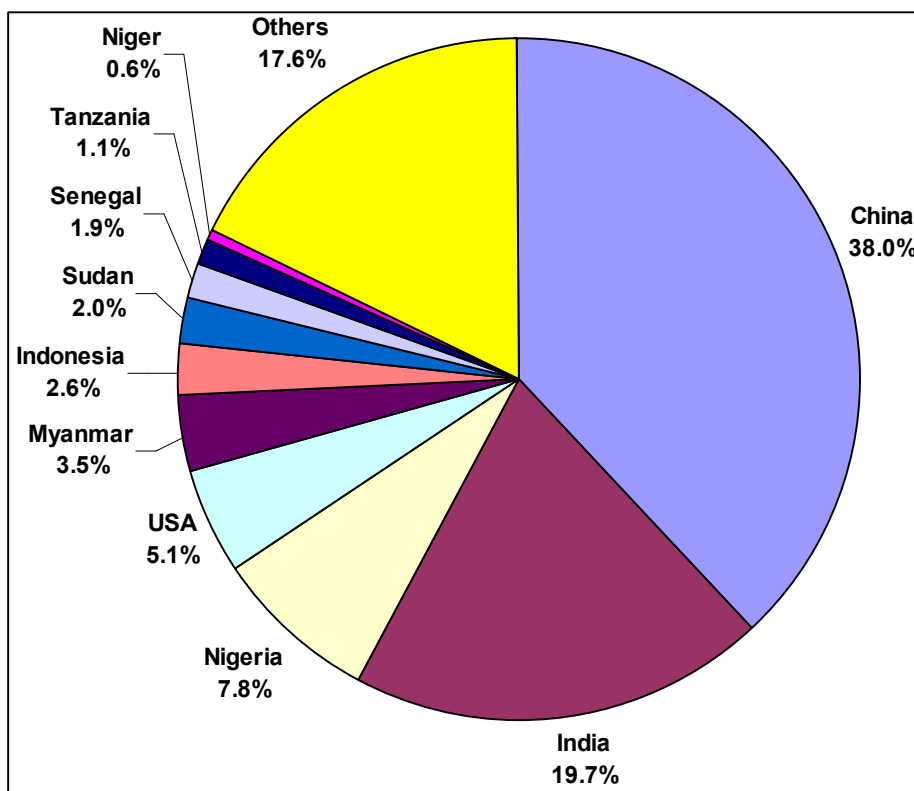
Important causes for agricultural drought are inadequate precipitation, erratic distribution, long dry spells in the monsoon, late onset and early withdrawal of monsoon along with lack of proper soil and crop management. Drought is the major abiotic constraint affecting groundnut productivity and quality worldwide. Groundnut plants are drought tolerant because of deep rooting and a water supply-related flexibility in time of flowering and fruiting.

The commercial groundnut cultivation is mainly in Asian (47 per cent of the world groundnut area contributing 62 per cent of the total world production), African (46 per cent area, 28 per cent production) and American (4.8 per cent area and 8 per cent production) countries due to suitable environment and photoperiod matching to the growing season. Though grown in limited area, the productivity of Cyprus (<100 ha area) is highest (>12000 kg ha<sup>-1</sup>) followed by Israel (2600 ha and 6440 kg ha<sup>-1</sup>) in the world mainly due to favourable season and high management. On the other hand the productivity of many African countries, are still around 400 kg ha<sup>-1</sup> mainly due to scanty rainfall (FAO, 2012).

In India generally the groundnut is grown as rainfed crop during rainy season (Kharif) with one or two protective irrigation as it encounter drought and also during Rabi, summer and spring seasons as a irrigated crop. The groundnut, is grown in about 270 districts of India, mostly as rainfed dry lands crop on well drained soils, under vagaries of the weather and only about 25 per cent of its area is irrigated. Presently, Gujarat (30 per cent total area and 36-40 per cent of production), Andhra Pradesh (28 per cent area and 20-28 per cent production), Tamil Nadu (7 per cent area and 11 per cent of production), Karnataka (14.5 per cent area and 10 per cent of production), Rajasthan (6 per cent area and 8.2 per cent of production) and Maharashtra (6.1 per cent area and 5.5 per cent of production) are the main groundnut growing states. The other states growing groundnut are Madhya Pradesh, Orissa, Uttar Pradesh and West Bengal. The occurrence of drought is a major cause of low groundnut productivity.

**Table 1.1: Global Scenario of Groundnut Production.**

Country	Area (lakh ha)	Production (lakh tonne)	Yield (kg/ha)
China	44.04	149.38	3390
India	55.20	61.06	1105
Nigeria	25.36	28.26	1119
USA	5.17	19.67	3796
Myanmar	8.40	13.36	1590
Senegal	10.30	10.16	975
Indonesia	6.43	7.76	1240
Niger	6.86	3.22	466
World	240.05	375.11	1562

**Figure 1.1: Global Scenario of Groundnut Production.**

Groundnut is an important crop of the semi-arid tropics where potential yields are frequently reduced by heat and water stress. Studies on occurrence and intensity of the drought during crop growing season revealed the effect of moisture stress on the groundnut yields in the dry lands. The groundnut is relatively drought resistant

and important crop of semi-arid regions where evaporation exceeds precipitation for 5-10 months of the year. The productivity (average of both the season) of groundnut during the year 2001 to 2010 though ranged from 700-1460 kg ha<sup>-1</sup>, in three major groundnut growing states, accounting for about 75 per cent of the total productivity of the country, the productivity was in between 1473-2390 kg ha<sup>-1</sup> in Gujarat, 1400-2130 kg ha<sup>-1</sup> in AP and 2100-3730 kg ha<sup>-1</sup> in Tamil Nadu during rabi-summer season, but fluctuated in between 510-2270, 300-1360, 1150-1880 kg ha<sup>-1</sup>, respectively in these states during kharif season mainly due to scanty rainfall. Presently, the average productivity of rabi-summer groundnut is about 1850 kg ha<sup>-1</sup>, much higher than kharif season (1410 kg ha<sup>-1</sup>) indicating more production potential during this season.

**Table 1.2: Area, Production, and Yield of Groundnut in India Since 2001.**

Year	Kharif			Rabi/Summer			Total		
	A	P	Y	A	P	Y	A	P	Y
<b>2001-02</b>	54.6	56.2	1030	7.8	14.1	1808	62.4	70.3	1127
<b>2002-03</b>	52.7	30.9	587	6.6	10.3	1548	59.4	41.2	694
<b>2003-04</b>	57.9	52.6	909	8.5	15.1	1771	66.4	67.7	1020
<b>2004-05</b>	52.0	68.6	1320	7.9	12.7	1602	59.9	81.3	1357
<b>2005-06</b>	57.4	63.9	1097	10.0	17.0	1702	67.4	79.9	1187
<b>2006-07</b>	47.8	32.9	689	8.4	15.7	1880	56.2	48.6	866
<b>2007-08</b>	53.0	74.8	1412	11.1	18.8	1691	64.1	93.6	1460
<b>2008-09</b>	52.3	56.4	1077	9.9	17.0	1726	62.2	73.4	1180
<b>2009-10</b>	46.2	38.5	835	8.6	15.8	1830	54.3	54.3	991
<b>2010-11</b>	49.8	66.4	1335	8.8	16.2	1846	58.6	82.7	1411
<b>Average</b>	52.4	54.1	1032	8.8	15.3	1739	61.1	69.3	1134

A: Area (lakh ha); P: Production (lakh tonnes); Y: Yield (kg/ha).

Twenty years of rainfall data at Tirupati for drought classification using aridity index on annual and monthly basis correlated groundnut yields were low due to uneven distribution of rainfall during crop growing season and moisture stress during July and September coincided with moisture critical periods (Sumathi and Subramanyam, 2007).

On deep well-drained sandy soils studies on water use and yield response of groundnuts for three years reveals that, yields were not reduced by droughts of short duration unless the seasonal water use was below 500 mm, however the pod yields were 2.26, 3.00 and 3.82 t/ha with approximately 330, 400 and 460 mm water, respectively (Hammond *et al.*, 1978). The field studies at ICRISAT for 5 years, the groundnuts advanced breeding lines produced greater pod yields on Vertisols (2.02-3.81 t/ha) than on Alfisols (0.61-1.56 t) and there was a strong soil type x genotype interaction. In another study, 4 cultivars water stressed during flowering, pod-set or pod-filling showed that while CGR were greater on Alfisols, these were linearly related to those measured on Vertisols. However, pod growth rates and partitioning

of DM to pods showed a strong soil type x genotype interaction and the genotypes developed on the Alfisol maintain relative ranking for total DM on Vertisol, but not necessarily for pod yields (Rao *et al.*, 1992).

For groundnut improvement in India at three regions (Hyderabad, Anantapur and Gujarat), the response relationships between yields and relative available water were estimated and empirical yield distributions were simulated and the alternative risk approaches compared with the traditional stability analysis and recommendations were presented by Bailey and Boisvert (1989). The rainfall data from 1981 to 2003 were categorized into excess, normal, deficit and drought years to know the vegetation cover due to variation in rainfall and identification of the land-use areas facing drought risk, using advanced very high resolution radiometer (AVHRR) sensor's composite dataset for analysing the temporal and interannual behaviour of surface vegetation and land-use classes - crop land (annual, perennial crops), scrub land, barren land, forest land, degraded pasture and grassland were identified using satellite data for excess, normal, deficit and drought years. Normalized difference vegetation indices (NDVIs) derived from satellite data for each land-use class in the drought year, the groundnut crop (0.267) showed the maximum, but the grassland recorded the lowest value of NDVI in all years. The groundnut (0.398), pulses (0.313), sorghum (0.120), tapioca (0.436) and horse gram (0.259), registered higher NDVI values than the perennial crops for the normal year. Among land-use classes, the groundnut witnessed the maximum values of 78.2, 64.5 and 55.2 per cent for normal, deficit and drought years, respectively. The vegetation condition index (VCI) used to estimate vegetation health and monitor drought. Based on the VCI classification, all land-use classes fall into the optimal or normal vegetation category in excess and normal years, whereas in drought years most of the land-use classes fall into the drought category except for sorghum, groundnut, pulses and grasses. These crops sorghum 39.7 per cent, groundnut 55.2 per cent, pulses 38.5 per cent and grassland 38.6 per cent registered maximum VCI values, with sustained under drought conditions suggesting that the existing crop pattern be modified in drought periods by selecting sorghum, groundnut and pulses crops and avoiding onion, rice and tapioca (Muthumanickam *et al.*, 2011).

Drought stress tolerance is seen in almost all plants but its extent varies from species to species and even within species. At whole plant level the effect of stress is usually perceived as a decrease in photosynthesis and growth, and is associated with alteration in carbon and nitrogen metabolism (Mwanamwenge *et al.*, 1999). Drought stress affects the growth, dry matter and harvestable yield, but the tolerance of genotypes to this menace varies remarkably. Quantification of the impact of drought on production of five major kharif crops (rice, groundnut, cotton, bajra, soyabeans), using the standardized precipitation index (SPI) that captures cumulative rainfall deviations at various time scales, computed for 36 meteorological sub-divisions using monthly rainfall data for the period of 1971-2002, identified July as the most drought affected, followed by September, while June and August were near normal. The Correlation between production of major kharif crops (1980-2001) and SPI values reveals that September was the crucial month for defining the crop yield for most of the Kharif crops throughout the country (Chaudhari and Dadhwal, 2004).

## 2.2 Radiation, Energy and Heat Flux

Estimation of surface sensible and latent heat flux is the most important to appraise energy and mass exchanges among atmosphere, hydrosphere and biosphere. The surface energy fluxes were measured by Kar and Kumar, (2007) over irrigated groundnut during winter (dry) season using Bowen ratio (beta) micrometeorological method in a representative groundnut growing areas of eastern India, at Dhenkanal, Orissa by growing the crop with four irrigations based on phenological stages (branching, pegging, pod development and seed filling) and assessed the crop stress at those times to see if irrigation scheduling could be optimized further. The net radiation  $R_n$  varied from 393-437 to 555-612  $W m^{-2}$  during two crop seasons. The soil heat flux ( $G_n$ ) was higher (37-68  $W m^{-2}$ ) during initial and senescence growth stages as compared to peak crop growth stages (1.3-17.9  $W m^{-2}$ ). The latent heat flux (LE) showed apparent correspondence with the growth which varied between 250 and 434  $W m^{-2}$  in different growth stages. The diurnal variation of Bowen ratio (beta) revealed that there was a peak in the morning (9.00-10.00 a.m.) followed by a sharp fall with the mean values varied between 0.24 and 0.28. The intercepted photosynthetic photon flux density or photosynthetically active radiation (IPAR) by the crop was measured and relationship between IPAR and leaf area index (LAI) was established with DAS, which is useful in developing algorithm of crop simulation model for predicting LAI or IPAR. The stressed and non-stressed base lines were also developed by establishing relationship between canopy temperature and vapour pressure deficit (VPD). With the help of base line equation,  $[(T_c - T_a) = -1.32VPD + 2.513]$ , crop water stress index (CWSI) was derived on canopy-air temperature data collected frequently throughout the growing season. The soil moisture depletion during the crop period when plotted with CWSI at different stages the values of CWSI varied between 0.45 and 0.64 just before the irrigations were applied and at two stages (branching and pegging), CWSI were much lower (0.46-0.49) than that of recommended CWSI (0.60) for irrigation scheduling (Kar and Kumar, 2007).

Studies on radiation and energy budgets over a cropped surface in the Sabarmati river basin, Gujarat, India by recording continuous data on temperature, humidity, wind speed and direction at 1 and 4 m on a 9 m tower, soil heat flux sensible and latent heat fluxes from March to August 1997, a polynomial relationship between residual flux and biomass under different phenological phases was observed, a linear relationship was found between residual flux and plant height under different phenophases and the biomass of crops increased exponentially with increasing AE: PE ratio and a polynomial trend was observed in water deficit, biomass and height (Padmanabhamurty *et al.*, 2001). The groundnut production was directly proportional to light interception and to the ratio between water lost and the vapour pressure deficit from leaf to air. Root growth and development was favoured under limited water supply and high water demand. Leaf conductance to gas exchange were similar at different combinations of soil water content and atmospheric saturation deficit (Goncalves de Abreu, 1988).

## 2.3 Water-yield Relationship

The evapotranspiration-yield relationships has a strong interaction with timing of drought and drought imposed at (a) emergence to maturity, (b) emergence to peg

initiation, (c) start of flowering to the start of seed growth, and (d) from the start of seed growth to maturity during the post-rainy seasons, the amount of water applied during these phases varied in groundnut cv. Robut 33-1 and the greatest reduction in seed yield (28-96 per cent) occurred when stress was imposed during (d), however, decreased irrigation during (b) increased pod yield over fully irrigated control by 13-19 per cent (Rao *et al.*, 1985). The crop coefficient curve facilitates the prediction of groundnut ET in preparation of planting at a new site from estimates of reference crop ET. The crop coefficient (Kc) values of groundnut at different crop-growth subperiods were influenced by evapotranspiration deficits and leaf area development of the crop. On a sandy loam soil of Hyderabad, in fully irrigated crop (W-W-W) the Kc value was low (0.564) during the establishment of plant (0-10 DAS), increased linearly through vegetative period and remained constant at 1.024 from flowering to start of the pod filling period (35-80 DAS), then decreased through pod filling period and reached a lowest value of 0.547 during the final 10 days of the crop period (Devi and Rao, 2003).

A study was conducted to characterize the plant extractable water pattern at four locations in India (Tirupati, ICRISAT, Jalgaon and Junagadh) and one location in Queensland, Australia (Kingaroy) and explore the possibility of clustering the multi-location trial environments based on similar water stress patterns. The APSIM groundnut model was used to compute daily changes in plant extractable soil water ( $P_{esw}$ ) at each site, by using climate parameters (ambient temperature, radiation, rainfall or irrigation amounts), soil hydraulic parameters and crop parameters (planting and harvest dates). Results from the  $P_{esw}$  characterization of experimental sites clearly demonstrated that the crops grown at the multi-location have experienced a wide variation in timing, intensity and duration of crop water deficits during the growing season and that quantification of the  $P_{esw}$  during the growing season and clustering of environments based on  $P_{esw}$  patterns can assist in understanding the basis of G x E interactions for yield between clusters, and to examine the effect of breeding methods on yield variation within each of the clusters (Rachaputi, 2003).

In Eastern India (Bhubaneswar) during dry season (November-March), the daily moisture use rate, increased gradually and reached the peak value (4.10-4.94 mm) during 55 to 60 days in groundnut cv. AK12-24 where the crop coefficient values followed the same trend as that of crop Et, which were lower at the initial growth stage (0.61-0.80), increased gradually and attained the maximum value of 0.94-1.33 towards the peak period of crop growth and declined thereafter. The crop coefficient value approached unity or slightly exceeded it during the maximum growth stage of the crop. Plants stressed at the early vegetative stage showed lowest crop coefficient value (0.61) at initial stage and the highest value (1.33) at peak crop growth stage, and withholding irrigation at an early stage (14 DAS) resulted in lesser evaporation of water from the soil surface (Kar *et al.*, 2001).

Field data on pod yield and seasonal ET as influenced by irrigation schedules during the summer predicted that the pod initiation and development stage (70 d to harvest) was the most sensitive stage for moisture stress with a yield response factor of 2.10. Water stress during 10 to 40 d was beneficial in enhancing pod yield with a yield response factor of 2.10 (Ramachandrappa and Nanjappa, 1994). During winter

at Rajendranagar, Hyderabad, in groundnut cv. ICGS 44 reproductive stage (35-115 DAS) was the most sensitive to a reduction in water supply, whereas water stress in the vegetative stage (10-35 days) had the least effect (Reddy *et al.*, 1996). At Coimbatore, TN, during summer 1994, water stress in groundnuts cv. Co 2 and VRI 2 at flowering, pegging, pod development or pod maturation when compared water stress at pod development was most detrimental on yield (Velu, 1998).

In Western India, a lysimeter experiment on black calcareous vertic Inceptisol at Junagadh, two groundnut cultivars subjected to water stress from the seedling to flowering (24-48 DAE), flowering to pegging (40-60 DAE), pegging to pod development (55-75 DAE) or pod development to maturation (75-95 DAE) decreased pod yields compared with plants given normal irrigations however yield reductions were greatest with stress imposed during the pegging and pod development and lowest with stress imposed from pod development to maturation (Patel and Golakiya, 1988). Further lysimeter trials on Spanish bunch groundnuts cv. J11 and GG 2 revealed that water stress from pegging to pod development gave the lowest pod yields with increased leaf temperature (35°C) markedly lowering photosynthesis. In all stress treatments, GG 2 out yielded J 11 mainly due to lower fluctuations in leaf temperature, stomatal resistance and lower vegetative growth (Patel and Golakiya, 1993). In another lysimeter studies, groundnut subjected to soil moisture tensions (SMT) of 330, 530 or 730 mbar, maximum daily water consumption occurred at 50-80 and 50-65 days in groundnuts grown at the 2 lower and the highest SMT, respectively and increase in SMT decreased total DM yield, but increased unshelled nut yields (Vivekanandan and Gunasena, 1976).

The total dry matter at harvest had positive correlation with TE, leaflet size was negatively correlated with TE under drought stress, the N content in leaves at 80 DAP and the chlorophyll content in leaves during moisture stress (28 days after imposing stress) showed positive relationship with TE. The leaf temperature 28 days after imposition of moisture stress had significant negative relationship with TE under adequately irrigated and simulated drought treatments. The mineral ash content of leaves 80 DAS in Spanish cultivars (ICG 476, ICG 221, ICG 1697, ICGV 86031 and TAG 24) had significant positive correlation with TE in simulated drought treatment (Babitha and Reddy, 2001). Sharma *et al.* (1987) studied the performance of two groundnut cv. under soil moisture stress during rainy season where number of gynophores and pods/plant, 100-seed wt, pod yield and shelling percentage were highest with two irrigations at 50 and 80 DAS and were lowest under rainfed conditions. Irrigation at 80 DAS was more effective than irrigation at 50 DAS. The moisture stress suppressed pod setting more in cv. M 13 than in cv. M 37. Oil content in seeds was not affected by moisture stress in both cultivars.

Studies on water-yield relationship in groundnut showed the yield response factor ( $k_y$ ) 0.45 and 0.42 under normal irrigation and 1.72 and 1.70 at full deficit irrigation during summer and Rabi seasons, respectively and the pod formation and flowering stages were more sensitive to moisture stress and irrigation during these stages is more important to overcome the yield reduction in groundnut (Thiyagarajan *et al.*, 2010). The groundnut cv. SB 11 grown at 3 levels of water stress applied at 4 growth stages, water stress of 0.8 (ratio of IW: CPE) at any growth stage reduced pod

yield, Maximum pod yield obtainable (3.06 t/ha) was predicted to be obtained with 1131 mm irrigation water (Shinde and Pawar, 1982).

The potential (no-water stress) and the lowest (no irrigation) yields for maize, soyabean and groundnut were calculated using three crop growth and water use models - CERES-Maize, SOYGRO, and PNTGRO where rainfall, temperature and solar radiation were used with these models to identify the 15 most severe drought years in the 53 year record in a 36-county region of Georgia, USA. In the 15 driest years, simulated yield losses averaged 75 per cent for maize, 73 per cent for soyabean, and 64 per cent for groundnut. In irrigated crop acreage of the study area, simulated water withdrawals exceeded 3 million m<sup>3</sup>/day, on average, for most of the 130 days between late May and late September (Hook, 1994).

Groundnut drought adaptation mechanisms with a view to developing selection criteria for breeding require survey under (1) drought evasion (ability to complete the development cycle before water deficits occur), (2) drought avoidance (mechanisms such as modified root and leaf morphology which allow the plant to keep its tissues at a high water potential during drought) and (3) tolerance to drought (maintenance of potential turgidity by osmotic adjustments, and tolerance of desiccation due to properties of the cell membrane) (Annerose, 1988). Most breeding programmes in groundnut follow an empirical approach to drought resistance breeding, largely based on kernel yield. Recent advances in the use of easily measurable surrogates for complex physiological traits associated with drought tolerance encouraged breeders to integrate these in their selection schemes. However, there has been no direct comparison of the relative efficiency of a physiological trait-based selection approach (Tr) vis-a-vis an empirical approach (E) to ascertain the benefits of the former.

### **3. Impact of Water Deficit Stress on Vegetative Growth**

#### **3.1. Seed Germination and Seedling Growth**

Soil moisture and atmospheric saturation deficit had a large effect on seedling emergence and establishment in groundnuts and best emergence at suboptimum temp was obtained at 40-80 per cent field capacity (FC) (Goncalves de Abreu, 1988). In field groundnut seed germinate well when soil water tension in the surface 30 cm was maintained at <0.6 bar during the growth of parent plants. Soil water tension >15 bar during the growing season reduced the germination of seed by 20, 5 and 5 per cent, of Florigiant, Florunner and Tifspan and yield of sound mature seed by 34, 22 and 7 per cent respectively (Pallas *et al.*, 1977). During germination the groundnut seeds remained in the imbibition phase for up to 25 h followed by a lag phase of 25-55 h and then entered into the germination or growth phase, the diffusivity of seeds increased up to 30 h of imbibition, then remained constant up to 55 h and thereafter again increased up to 75 h. Maximum soluble N and the break of oxygen concentrations constancy occurred at the 45 h of imbibition the time when germination was triggered which became visible 6-8 h later (Golakiya, 1989). About 35 per cent moisture is the minimum requirement to initiate the germination process however, germination time was curtailed by increasing seed moisture content and radical emergence in most seeds appeared at 55-60 per cent moisture content (Golakiya, 1989).



Ten crop species evaluated for their relative drought tolerance at the seedling stage by planting seeds in wooden boxes ( $130 \times 65 \times 15 \text{ cm}^3$ ) filled with soil by withholding water a week after germination and observing reaction to progressive water stress. Based on percent dead plants and days taken to 100 per cent dead plants, soyabean (*Glycine max*) was the most drought susceptible and cowpea (*Vigna unguiculata*) the most drought tolerant, however, ranking of crops in the increasing order of drought tolerance was: soyabean < black gram (*V. mungo*) < green gram (*V. radiata*) < groundnut < maize (*Zea mays*) < sorghum (*Sorghum bicolor*) < pearl millet (*Pennisetum glaucum*) < bambara nut (*V. subterranea*) < lablab bean (*Lablab purpureus*) < cowpea (Singh *et al.*, 1999).

The relative drought tolerance could be studied at the seedling stage by planting seeds in wooden boxes ( $130 \times 65 \times 15 \text{ cm}^3$ ) filled with different proportion of sand, loamy sand and sandy loam, irrigating daily till the establishment and withholding water a week after germination and observing reaction to progressive water stress by counting percentage dead plants at various time intervals and days taken to 100 per cent dead plants. Soil with higher sand content induced water stress and with increased clay content and gradual water stress, it may be possible to use this method to detect varietal differences in less drought tolerant crops (Singh *et al.*, 1999). In indoor and field experiments showed that germination potential and germination percentage, growth vigour and vitality index of groundnut seeds increased after soaking with 500 mg/litre of nitrate rare earth element solution (38.7 per cent of rare earth oxide) for 24 h before sowing. Seedlings emerged 1 or 2 days earlier, the emergence rate increased, drought resistance enhanced significantly under moisture stress resulting in strong seedlings and quick root development, leaf area, number of branches, chlorophyll content, proline content and photosynthetic rate also increased (Nie ChengRong *et al.*, 2002).

Water uptake, germination and seedling growth of 12 groundnuts cv. of 4 botanical groups studied under polyethylene glycol 6000 which simulated moisture stress (-1 to -10 bar water potential) water uptake by seeds showed no differences amongst botanical groups in spite of varietal differences (Babu *et al.*, 1985). The simulated water stress by PEG 6000 decreased groundnut germination, germination relative index and vigour index, seeds did not germinate at -10 bar, the activities of acidic and alkaline lipases and protease increased with the progression of germination but decreased with an increase in the stress level. Peroxidase activity was negligible in the cotyledons as well as in the embryonic axis up to day 1 of germination but increased thereafter, increasing level of stress decreased the enzyme activity (Sharma *et al.*, 1987). Seeds of 20 groundnut cultivars watered with a hyperosmotic solution, 20 per cent PEG 6000 at 25°C, and after 8 days, germination percentage, radical root length and dry weight indicated that germination characteristics of groundnuts grown in hyperosmotic solution may be useful as indicators for selection for drought-resistant genotypes (Xue *et al.*, 1997).

Germination studies on four groundnut cultivars (Ex-Dakar, RRB 12, RMP 12, RMP 91) under different osmotic solutions when compared with some agronomic and yield parameters of plants grown under simulated drought conditions in the field, indicated that germination of seeds in polyethylene glycol (PEG), glucose or

sodium chloride (NaCl) solutions at 1.2 MPa and 1.8 MPa could be reliably used as a quick and cost effective procedure for screening groundnut cultivars for drought resistance at an early stage of their growth and development and maximum germination percentage, radicle length and dry weight were attained in RMP 91 and Ex-Dakar identified as drought resistant (Mensah and Okpere, 2000). Susceptibility to drought was shown by the relatively greater reduction in yield per plant compared to the resistant cultivars. The PEG-induced water stress imposed by treating the seeds at different water potentials (-0.3, -0.6 and -1.0 MPa) on 10 different groundnut cultivars (TCGS 20, GG 2, TMV 2, JL 24, ICGV 86031, K 134, TAG 24, JL 220, CSMG 84-1 and TCGS 41), showed significant reduction in germination, seedling growth and seedling vigour index with the decreasing water potential from -0.3 to -1.0 MPa. Among the cultivars, ICGV86031 showed the highest resistance to water stress and germination and seedling growth even at the -1.0 MPa where all other cultivars completely failed (Prathap *et al.*, 2006).

In groundnut seedlings of different habit groups for 15 days, the total polyamine level in the root and shoot varied from 2.5-4.9  $\mu$  mol/g fresh weight and 2.8-4.6  $\mu$  mol/g fw, respectively. In each habit group, roots of GG 2, G 13 and G 20 showed the highest total polyamine content and in the shoots, similar results were obtained except among the spreading cultivars, M13 recorded the highest polyamine content. Artificial stress (PEG 6000) increased the polyamine content in both root and shoots, however, putrescine application just before PEG stress prevented the fall in tissue moisture content in water-deficit seedlings (Vakharia *et al.*, 2003).

Germination of spp. under simulated drought (0.10 bar osmotic pressure) was in the order *D.tortuosum*>*Crotalaria spectabilis*>soyabean>groundnut. In field trials, the emergence frequency was higher during the sowing dates for groundnut than those for soyabean where drought reduced groundnut seed yields by 83 kg/ha (Hoopper, 1978). In a field trial with 3 groundnut cultivars, the seed hardening with 1 per cent calcium chloride or 2 per cent  $\text{KH}_2\text{PO}_4$  was most effective, but germination was adversely affected by seed treatment with 1.5 per cent succinic acid (Arjunan and Srinivasan, 1989). The better performance of seedlings of groundnut cv. RS 218 than of cv. MGS7 under soil moisture stress conditions when grown from seeds treated with 0.25 per cent  $\text{CaCl}_2$  for 8 h was ascribed to a markedly higher accumulation of proline and K in seedlings of RS 218 (Sashidhar *et al.*, 1981).

The bunch groundnut, *Arachis hypogaea* subsp. *fastigiata*, varieties show little seed dormancy and 20-50 per cent of pods germinate in situ due to rains at the pod maturity stage. At Aliyarnagar, 55 high yielding genotypes of subsp. *fastigiata* when grown in the field ICGV 86011, derived for the cross (Dh 3-20 X UAS20) X NcNc 2232, possessed seed dormancy, with pods sprouting 18 days after harvest compared with 2-4 days for the other genotypes. ICGV 86011 has also shown resistance to sucking pests (Varman and Raveendran, 1991).

Seeds of groundnut cultivars soaked in water or in solutions containing 50 ppm Ascorbic acid or 1 per cent calcium chloride for 15 h, dried and germinated in water and polyethylene glycol (at osmotic pressures of -5 and -10 bar) showed that seeds of cv. S 206 and BH 818 in water and cv. NG 268 in calcium chloride gave the highest

germination and root length which decreased with increase in osmotic concentration of the solution (Prasad *et al.*, 1974). The germinated 3-day-old seedlings of groundnut cv. Yueyou 551-116, seeds when treated with 5 ppm PP333 resulted in substantial accumulation of ABA in the leaves under both normal and water stress conditions, while the biosynthesis of GA was inhibited by PP333, as ABA and GA could be antagonistic due to competition for a common precursor. The PEG solution ( $10^{-3}$  mol PEG/litre), treated seedlings showed little change in plasmalemma permeability and in leaf water content whereas those of the control decreased markedly, suggesting that PP333 could increase drought resistance of groundnut plants (Li and Pan, 1988).

### 3.2 Crop Growth Rate and Dry Matter Production

In greenhouse the shoot and root growth and root stratification in the soil profile for groundnut, indicated that the leaf number and leaf area decreased and root/shoot ratio increased in response to water stress, greatest deepening of the root system in the soil profile in response to water stress (Pinto *et al.*, 2008). Nageswar Rao *et al.* (1993) discussed various parameters for selection of drought resistant varieties in breeding by taking 10 groundnut genotypes grown with adequate irrigation, and subjected to drought during pod filling (83-113 d after sowing) on a medium deep Alfisol at ICRISAT Centre, Andhra Pradesh, during post-rainy season. Shoot DM accumulation during the drought period was 72-150 g/m<sup>2</sup> and was closely related to transpiration. The groundnut cv. J 11 subjected to water stress for (a) 6 or (b) 9 days during the vegetative stage (after 30 days growth) or for (c) 6 or (d) 9 days during the reproductive stage (after 45 d), about 80 per cent of plants in (b) died and nodule numbers in (a), (c) and (d) were 47, 57 and 72 per cent, respectively, lower than that of unstressed controls immediately after rewatering and were 55, 28 and 66 per cent 15 days later. 15 days after stress relief, plant N content was only about 50 per cent of that of unstressed plants (Kulkarni *et al.*, 1988).

In field trials at Parbhani groundnuts sown in Feb., with 30 kg N, 60 kg P<sub>2</sub>O<sub>5</sub> and 30 kg K<sub>2</sub>O/ha and irrigated at different IW: CPE ratios, water stress at an IW:CPE ratio of 0.4 at the seedling stage, flowering, peg formation or maturity reduced number of branches/plant, pod yield and total DM yield (Shinde and Pawar, 1984). The effect of imposed single and double water stress on the growth and yield of three grain legumes, cowpea cv. IT 1627, groundnut cv. Kumawu Red, and Bambara groundnut (*Vigna subterranea* cv. *Jabajaba*) commonly grown in sub-Saharan Africa was studied by providing various treatments: liberal watering until maturity; 7-day dry cycle at 41-47 days after planting (DAP); and dry cycle at 41-47 DAP, followed by liberal watering and another dry cycle from 54-59 DAP. Water stress significantly reduced growth of both cowpea and Bambara groundnut but not groundnut. Groundnut was the most tolerant of post-flowering water stress among the three legumes (Kumaga, 2003).

Groundnut cv. JL 24 was sown on 15 January, 15 February and 15 March at two (50 cm x 6 cm and 25 cm x 12 cm) spacing, and irrigated once during the first phase of flowering (I1), twice during the first phase of flowering and pod initiation (I2) or thrice during the first phase of flowering, pod initiation and development (I3) at Kalyani, West Bengal, India the nodules per plant (78) and nodule dry weight per

plant (140) at 90 DAS, as well as pod dry weight (5.88) at 110 DAS, and pod (2336 kg/ha) and haulm yield (6330 kg/ha), were highest in the crop sown on the 15 February. Irrigation had no significant effect on the number of nodules per plant and nodule dry weight at 30 and 90 DAS. However, I3 recorded the highest shoot (21.57 g/plant) and pod dry weight (5.68 g/plant) at 110 DAS, and pod (2420 kg/ha) and haulm yield (6520 kg/ha). Water stress at the pod initiation and development stages reduced pod yield by 13.4 and 44.2 per cent, respectively. Spacing at 25 cm x 12 cm recorded a higher number of nodules per plant at 90 DAS, nodule dry weight per plant, shoot and pod dry weight at 110 DAS and pod yield compared to the 50 cm x 6 cm spacing. Spacing had no significant effect on the haulm yield (Patra *et al.*, 1999). Six groundnut cultivars were grown at Akola, Maharashtra in kharif [rainy] season on deep soil (>120 cm) with 50 per cent water holding capacity or on shallow soil (<20 cm) with 30 per cent water holding capacity. Water stress occurred during the vegetative (-16 bar) and reproductive (-14 bar) growth stages on shallow soil. Water stress decreased root growth, nodule number and DW, pod yield, seed number/plant and shelling percentage (Dhopte *et al.*, 1992).

The rate/temp relation of several developmental processes in groundnut examined in greenhouses at air temp of 19, 22, 25, 28 or 31°C and also the sensitivity of the processes to soil water deficit was examined by applying 30 mm of irrigation immediately after sowing and when tensiometer readings at 0.1 m depth exceeded 20 kPa (wet soil treatment). The relation between rate and temp was linear and the measurements when analysed in terms of thermal time an extrapolated base temp ( $T_b$ ) was 10°C at which the rate was zero for leaf appearance, branching, flowering, pegging and podding. Leaf appearance and branching were more sensitive to soil water deficit than the other processes examined (Leong and Ong, 1983). Thirty-three groundnut genotypes evaluated under water stress during summer at Bangalore showed wide variability for most of the characters studied. The estimates of PCV and GCV were high for primary branches per plant, biomass per plant and shoot root ratio. Heritability was high for plant height, root-shoot ratio, number of primary branches per plant and number of pods per plant under water stress condition than under non-stress situation. A relatively higher genetic advance as per cent of mean was noticed for plant height, shoot-root ratio, number of secondary branches per plant, number of pods per plant and biomass under water stress conditions under non-stress conditions (Ravi *et al.*, 2008).

The growth and agronomic traits of 18 groundnut cultivars under waterlogging during late vegetative to flowering stage when analysed, waterlogging decreased plant height, number of branches, total pods and full pods, however it promoted pod growth and the ratio of seeds that developed into full pods. Cluster analysis based on agronomic traits was somehow integrated with yield classification after waterlogging (the 18 cultivars classified into 6 types). The most tolerant cultivars (HT type) selectively bred under waterlogging were dwarfed with synchronously increasing number and weight of pods and seeds and promoted the ratio of full pod number and ratio of full pod weight. The findings illustrated that waterlogging tolerant eco-breeding was effective. Because more water was demanded in the late vegetative to flowering stage, the impact of waterlogging was limited and even promoted pod and seed development

for most waterlogging tolerant cultivars so long there was water flow and groundnuts not completely submerged. Therefore, groundnut flood impact assessment should focus on flood intensity, growth and development period and varietal tolerance (Wang *et al.*, 2009).

In medium black calcareous soil (Typicustochrepts) groundnut cvGG 2 during summer given cyclic water stress at four stages *i.e.*, flowering ( $S_f$ ), pegging ( $S_{pg}$ ), pod formation ( $S_{pf}$ ) and pod development ( $S_{pd}$ ) and three levels of potassium (0, 20 per cent  $K_2O$  as foliar spray and 60 kg  $K_2O$  ha<sup>-1</sup> as soil application), water stress at pegging or its association with any one or two phenophase(s) reduced the accumulation of dry matter and nutrients, while pod yield was most adversely affected due to water stress during pod development stage. The accumulation of all the nutrients increased with advancement of crop growth except K in which the maximum accumulation was found at 78 DAS. Foliar application of potassium only increased its uptake, while soil application increased N and K uptake by the crop (Sakarvadia *et al.*, 2010).

The crop evapotranspiration (ET) and growth characteristics of groundnut in the transitional humid zone of Nigeria have shown that the total water used (ET) by the crop during 105 days was 303 mm and more amount of water was used between the vegetative and reproductive growth stages of the crop between 20 and 60 DAP, the highest mean leaf area (LAI) obtained was at 75 DAP, dry matter accumulation was highest between 75 and 90 DAP when canopy radiation interception was between 70 and 80 percent and there was a positive correlation ( $p=0.01$ ) between growth parameters and water use (Idinoba *et al.*, 2008).

### 3.3 Flowering and Peg Formation

In groundnuts flower production ceased when water stress started, but recovered as soon as plants were rewatered, especially with early drought. A 5-day drought period was most damaging in terms of flower and pod numbers and av. plant wt when imposed 5 weeks after sowing and decreased seed yield from 106-107 (control) to 43-92 g/m<sup>2</sup> (Zaharah, 1986). Several groundnut cv. when grown in field at water deficit during early peg and pod formation (40-82 days), even after re-watering, plants subjected to drought were 3-5 nodes shorter than normal plants and peg and pod numbers at 77 DAS were 51 per cent lower than normal, pod maturity was delayed by 10-11 days (Boote and Hammond, 1981). The flush of late flowers following mid season drought delay maturity. Flowering stopped when soil moisture dropped to wilting point, but fruiting continued (Scandalariis *et al.*, 1978). The fruiting occurs once the gynophores enter into the soil. The soil physical condition is important and must be wet during the gynophore entering the soil as the gynophore can exert a force equivalent to 3-4 g only.

In a field during summer, groundnut cv. TMV2, moisture stress at various stages of development did not reduce the total number of flowers formed, but reduced the number of gynophores formed from the 1<sup>st</sup> flush of flowering. However, yield from the 2<sup>nd</sup> flush compensated so that the total pod yield was not affected by moisture stress treatment. Moisture stress in the early flowering phase (30-45 DAS) was not critical when soil MC was <30 per cent in the top 90 cm (Gowda, 1977). Also in a field trial,

Gowda and Hegde (1986) found that total flowers produced by groundnut plants subjected to soil moisture stress (SMS) between 30-45 DAS were not different from those produced by regularly irrigated plants. The SMS decreased pod yields by 4.7 per cent, as the first flush of flowers produced up to 45 DAS dried up and did not form gynophores. However, a higher percentage of fruit set from the 2<sup>nd</sup> flush compensated for yield differences.

Flowering pattern and total flowers produced in 6 bunch type groundnut cvs. subjected to intermittent cycles of moisture stress and gynophore length at harvest as an index of pod ontogeny was related to the number and synchrony of flowers produced during any growth period and the proportion of pods produced at different growth stages determined based on gynophore length is suggested as a selection index by Janamatti *et al.* (1986) where the cv. did not differ in the total number of flowers produced/plant in any of the moisture regimes, indicating that the number of flowers was not a constraint in productivity even under moisture stress. Gynophore length of potential pods indicated that under severe stress, only the early formed flowers developed into pods. In stressed plants although the total number of pods decreased, the percentage of total pods with a gynophore length of 0.1 to 3.0 cm increased markedly and in some cv. it was about 55 per cent. A significant burst in flowering on alleviation of stress was the unique feature in the pattern of flowering under moisture stress, particularly when it was imposed just prior to the reproductive phase (Janamatti *et al.*, 1986).

In groundnuts, the leaf area, number of flowers and gynophores, haulm and pod yields, dry wt. of root, RWC of leaf and leaf-water potential decreased continuously with an increase in soil moisture stress from 0-0.3 to 0-14 bar in the greenhouse and from 0-0.5 to 0-20 bar in the field (Patel *et al.*, 1983). A stress of 10 bar at the flowering, pegging and pod-development stages was harmful for haulm and pod yields. When the soil surface was kept dry and the crop was irrigated from the bottom of a pot through soil capillary flow, pod yield was low but haulm yield and number of pegs and flowers were max., indicating that a hard soil hinders gynophore penetration. On re-watering after stress, both leaf area and number of flowers increased simultaneously. Within 40 days from the onset of flowering the crop had put forth 63 per cent of all the flowers produced during the entire period of its growth (Patel *et al.*, 1983).

In field trials in Ceara, Brazil, groundnuts cv. PI 165-317 from the USA, PI 55437 from Senegal and Tatu from Brazil grown on sandy soil and sprinkler irrigated to 100, 88.5, 73 or 61 per cent of the water depth required at soil matric potential of -0.05 MPa reveals that increasing water stress reduced leaf area, number of leaves and flowers, shelling percentage and reproductive efficiency. With 100 per cent irrigation flowering peaked after 5 weeks, but severe water stress shortened this to 2 weeks. Transpiration and yield were correlated with soil water deficit and pod yield was highest for PI 165-3176 under all water regimes (Ferreira *et al.*, 1992). The management practices should aim to optimize the availability of growth resources at the time of pegging in order to ensure that pod initiation is not delayed.

### 3.4. Leaf Area, SLA, SPAD and Stomatal Studies

Water stress reduces the leaf area, leaf area duration, chlorophyll content and stomatal frequency and this effect varied with stress in the early and late in the growing season. In Bangalore, groundnut irrigated at 0.4, 0.6 or 0.8 CPE during summer the leaf area duration and pod yield increased with increasing irrigation level (Sridhara *et al.*, 1998). Irrigation at 0.8 CPE gave the highest DM accumulation, leaf area and LAI (Sridhara *et al.*, 1995). However, complex nature of physiological traits associated with drought tolerance and the difficulties associated with their measurements in segregating large populations inhibit their use in developing water-use efficient genotypes in breeding programmes. The easily measurable surrogates of transpiration efficiency (TE), a trait associated with drought tolerance - specific leaf area (SLA) and soil plant analytical development (SPAD) chlorophyll meter reading (SCMR), it is now possible to integrate TE through the surrogates in breeding and selection schemes in groundnut. As a noninvasive surrogate of TE, SCMR is easy to operate, reliable, fairly stable and low cost.

Nigam and Aruna (2008) in a study evaluated the drought tolerant characteristic and as to what extent the SCMR measurements can be spread over time by evaluating 18 diverse groundnut genotypes for two physiological traits, SCMR and SLA in post rainy (Nov-Apr) seasons in India by recording observations at different times during and after the release of moisture deficit stress where there was general agreement in genotype and trait performance in both the seasons. The ICGV 99029 and ICR 48, which recorded higher SCMR and lower SLA values in both the seasons, were identified good parents for WUE trait in breeding programmes. Other good parents include ICGS 76, TCGS 647 and TCGP 6. The SCMR recorded at three different times under differing soil moisture deficit showed highly significant correlation with each other. Similarly, SLA at different times also correlated significantly with each other. SCMR and SLA were significantly negatively correlated with each other and the relationship was insensitive to time of observation (Nigam and Aruna, 2008). The SCMR and SLA observations can be recorded at any time after 60 days of crop growth, under moisture deficit conditions and gives groundnut breeders to record these observations in a large number of segregating populations and breeding lines in the field.

The LAI was not affected before 40-45 DAS but was reduced by 20-25 per cent in unirrigated plants between 60 DAS and final harvest (Black *et al.*, 1985). In cv. GAUG 1, water stress increased the leaf proline content and stomatal resistance and decreased nitrate reductase activity (NRA), RWC, transpiration and seed yield and application of 40 kg K/ha increased the proline content, stomatal resistance, NRA, RWC, DM accumulation and yield. Seed oil contents were higher in the water-stressed than in unstressed plants. K increased the oil contents in stressed and unstressed plants (Umar *et al.*, 1991). The RWC decreased with onset of water stress and with increase in plant age. The extent of decrease in RWC was greater in the control than in plants treated with antitranspirants; RWC was higher with Sunguard, alachlor and Rallidhan than other treatments (Amaregouda *et al.*, 1994). Rao *et al.* (1998), in a remote sensing ground truth experiment to monitor a groundnut crop under non-stressed conditions in Brazil (during Sept.-Dec.) reported that, the canopy reflectance

in the red and near infrared wave bands of the thematic mapper of two vegetation indices, soil adjusted vegetation index (SAVI) and the normalized difference vegetation index (NDVI) were correlated very well with both the LAI and biomass and can be used to estimate LAI and biomass of a groundnut crop.

The effects of elevated atmospheric CO<sub>2</sub>, in combination with water stress in groundnut cv. Kadiri-3 studied by Clifford, (1995) revealed that the effects of future increase in atmospheric CO<sub>2</sub> concentration on stomatal frequency in groundnuts are likely to be small, especially under water stress, but that the combination of associated reductions in leaf conductance and enhanced assimilation at elevated CO<sub>2</sub> will be important in semi-arid regions. The CO<sub>2</sub> exerted significant effects on stomatal frequency only in irrigated plants. The effects of drought on leaf development outweighed the smaller effects of CO<sub>2</sub> concentration, although reductions in stomatal frequency induced by elevated atmospheric CO<sub>2</sub> were still observed. Under irrigated conditions with unrestricted root systems, an increase in atmospheric CO<sub>2</sub> from 375 to 700 ppm. Decreased stomatal frequency on both leaf surfaces by up to 16 per cent; in water stressed plants, stomatal frequency was reduced by 8 per cent on the adaxial leaf surface only. Elevated CO<sub>2</sub> promoted larger reductions in leaf conductance than the changes in stomatal frequency, indicating partial stomatal closure. As a result, the groundnut stands grown at elevated CO<sub>2</sub> utilized the available soil moisture more slowly than those grown under ambient CO<sub>2</sub>, thereby extending the growing period. Despite the large variations in cell frequencies induced by drought, there was no effect on either stomatal index or the adaxial/abaxial stomatal frequency ratio (Clifford, 1995).

In central India Azam Ali, (1984) studied the interaction between population and water stress in 4 populations of groundnut by estimating, transpiration, stomatal resistance (rs), boundary layer resistance (ra), vapour concentration difference between leaf and air (deltachi) and LAI and the frequency distributions of rs, ra, deltachi and seasonal changes in LAI when plotted to analyse the dependence of transpiration rate on each variable both per unit area of leaf surface (E1) and per unit land surface (Ee), for estimates of E1, both rs and deltachi were of similar importance, exerting a far greater influence than changes in ra. However, in terms of Ee, changes in LAI were far more important than in any other variable, particularly late in the season when water was scarce. The ability of this technique to describe temporal and spatial variations as well as the dominant environmental and physiological influences on transpiration may outweigh any small loss in accuracy of estimates.

At Tirupati, India, Babitha, (2006) screened 111 Spanish and 110 Virginia groundnut genotypes for moisture stress and high temperature tolerance during post-rainy season, and classified into 3 groups, *i.e.* low, medium and high for SPAD chlorophyll meter reading (SCMR), SLA, chlorophyll fluorescence ratio and membrane injury, where majority of the Spanish genotypes had medium SCMR (45-50) and SLA (125-150), while most of the Virginia cultivars had high SCMR (>50) and medium SLA (125-150), majority of the Spanish and Virginia genotypes had high membrane injury of >60 per cent. Genotypic variation was observed for SCMR, SLA, chlorophyll fluorescence ratio and membrane injury. The Spanish genotype JAL 07 had a low membrane injury (37 per cent). Incidentally, it also maintained high SCMR (52) and



low SLA ( $101.6 \text{ cm}^2/\text{g}$ ), indicating that it can tolerate both water deficit and high temperature.

There is equal number of stomata both on the upper and lower epidermis of leaves in groundnut. Unlike other crops, in groundnut the stomata remains open during drought, but are more sensitive to light. The groundnut does not have complete stomatal control over transpiration loss but some control is achieved through folding and orientation of leaves parallel to the incoming radiation. Leaflet area, stomatal frequency, stomata number and stomatal size evaluated in seven groundnut cultivars in the summer and rainy seasons, the cultivars TAG 24 and Somnath, show higher WUE. In TAG 24, Somnath, TG 22 and TKG 19A, reduction of leaflet area was associated with increased stomatal number and frequency on the adaxial surface. However, no differences were observed for stomatal length and breadth. Reduced leaflet area with corresponding increase in stomatal frequency and number of stomata on adaxial surface appeared to be related to WUE in TAG 24 and Somnath (Badigannavar *et al.*, 1999).

In field at Redland Bay, Queensland, groundnut cultivars with reduced soil water supply (RSW) during early reproductive development, total biomass production of two Virginia type cultivars (Virginia Bunch and Q 18801) was greater than that of a Spanish type cultivar (McCubbin), the RUE and transpiration efficiency of Q18801 were significantly greater than those of McCubbin. The RUE of the stressed crops was only about 45 per cent of those that were fully irrigated. Throughout RSW, noon leaf water potential was lowest in McCubbin and under increasing soil water deficit, the leaves of McCubbin tended to wilt, while the Virginia cultivars displayed active leaf folding and the ratio of the fraction of radiation intercepted by the canopy to LAI was always lower in the Virginia type cultivars. For a given LAI, this phenomenon may have allowed these cultivars to decrease the effective atmospheric demand within the canopy, while maintaining radiation interception at saturation for photosynthesis. The consequence of this, given that the supply of water from the roots did not differ, was that Q18801 was able to maintain a higher LAI and greater crop transpiration efficiency (ratio of biomass production to transpiration) than McCubbin. Thus existence of differences among cultivars in transpiration efficiency under drought may prove useful in improving adaptation of groundnut to these environments (Chapman *et al.*, 1993c).

### 3.5. Leaf Water Potential, Transpiration, RWC and Osmotic Adjustment

The leaf area, which is in rapid growth stage during the vegetative and flowering stages tends to be most affected due to water stress causing reduction in photosynthesing surface and crop growth rate. The most common symptom of water stress in the fields is stunted growth as water stress first affects the cell enlargement rather than cell division, but long exposure of water stress inhibited cell division also. The stem length is reduced more markedly than leaf size and the leaf arrangement becomes more compact. During vegetative and reproductive stages the net assimilation rate is inversely proportional to LAI and it is possible to define optimum LAI for maximum dry matter production in particular area. Turgor potential ( $\psi_p$ ) and leaf extension rate (R) are reduced at high saturation deficits and R is linearly related

to  $\psi_p$  between 0900 to 1600 hr., in driest condition. The groundnut maintains high leaf water content even in dry soil and also continues photosynthesising at lower leaf water content than other crops.

The water flow in intact plant under high soil moisture condition is for growth and transpiration and two concepts are expressed about the driving force for transpiration water flow: one consider the water potential differences between the root and leaf as the primary force while the other consider hydrostatic and osmotic pressure differences as the factors determining water flow. In order to sustain plant growth and hydration, water must be continuously supplied to the leaves as it is lost by transpiration. This becomes difficult under low soil moisture condition. The ability of groundnut genotypes to maintain water supply to leaves measured by apparent sap velocity ( $V_a$ ) was 0.8-1.1 cm min<sup>-1</sup> and declined with stress in field (Ketring *et al.*, 1990).

The relative water content (RWC) is the water-relation component that seems most directly related to cell-hydration. Other factors such as osmotic adjustment and apoplastic water content contribute to cell turgor through maintaining high RWC and it can be readily measured for larger plant populations. Mild drought induces in plants regulation of water loss and uptake allowing maintenance of their leaf relative water content (RWC) within the limits where photosynthetic capacity and quantum yield show little or no change. The most severe form of water deficit is desiccation - when most of the protoplasmic water is lost and only a very small amount of tightly bound water remains in the cell. Groundnut has an enhanced capacity for maintaining leaf water content against a soil water deficit. However, RWC of the leaf did not recover to its original value on re-watering after severe stress. The leaf water potential and relative water content were negatively correlated with a correlation coefficient of -0.95. The linear regression equation was  $\Psi_L = 64.8 - 0.61 \text{ RWC}$ . Perceptibly, stressed plants have lower RWC than non-stressed plants. RWC of non-stressed plants ranged from 85 to 90 per cent, while in drought stressed plants, it may be as low as 30 per cent (Babu and Rao, 1983).

The RWC decreased in groundnut varieties upon induction of drought stress with sharp decrease, but in varieties K 1375 and R 9251 more than 90 per cent relative water content was observed with a decrease of 24 per cent RWC in K 1375 as compared to control, while 44 per cent of decrease was observed in R 9251 as compared to control (Sharada and Naik, 2011). Ramana Rao (1994) reported reduction in RWC of groundnut in both simulated stress and rainfed treatments compared to fully irrigated treatments at 9, 18 and 27 days after imposition of water stress. Increasing moisture stress from 0 to 2, 4 and 6 atm decrease the leaf RWC, increased water saturation deficit and relative saturation deficit, decreased DM accumulation in the shoot and increased it in the root, decreased RGR, increased specific leaf weight, decreased non-reducing sugar and increased reducing sugar in groundnut seedlings (Sharma *et al.*, 1985).

The stomata occupy a central position in the pathways for both the loss of water from plants and the exchange of CO<sub>2</sub> and thus provide the main short-term control of both transpiration and photosynthesis, though the detailed control criteria on which

their movements are based are not well understood and are likely to depend on the particular ecological situation.

Using simple models one can investigate the role of stomata in the control of gas exchange in the presence of hydraulic feedbacks and to clarify the nature of causality in such systems. Comparison of a limited number of different mechanistic models of stomatal function is used to investigate likely mechanisms underlying stomatal responses to environment. In greenhouse, a drought resistant groundnut cvs. Nigeria 55437 and IAC Tupa a drought sensitive one when compared, the Nigeria 55437 showed high leaf diffusion resistance ( $R_s$ ) and low leaf water potential ( $p_{siv}$ ) and transpiration ( $E$ ) when subjected to water stress, and had a high proline concentration ( $P$ ) even under irrigation. There were negative correlations between  $p_{siv}$  and  $R_s$ , and  $p_{siv}$  and  $P$ , and positive correlations between leaf temperature ( $T_f$ ) and  $R_s$ ,  $T_f$  and  $P$ , and  $R_s$  and  $P$  under water stress (Nogueira *et al.*, 1998). A biochemical test using 0.1M EDTA was developed for detection of moisture stress in youngest fully opened leaves, and the cultivars showing 2.77 per cent decline in the pH of the leaves extract in EDTA at -10 bar were categorised as drought tolerant (Dwivedi *et al.*, 1986). Leaves of groundnut have also been shown to accumulate proline under moisture stress (Misra *et al.*, 1992), the level of which was significantly correlated with the level of activity of glutamate-oxaloacetate transaminase in leaves (Yadav *et al.*, 1993).

Most part of India, shortage of water is caused by uneven distribution of rains, gaps between rain events and field water losses rather than from low seasonal or annual rainfall totals. The groundnut grown in the micro catchment during the rainy season, utilized 364-733 mm water in evapotranspiration ( $ET$ ) and deep percolation ( $P$ ) (Rathore *et al.*, 1996). In a water balance studies in M.P. in a 1.05 ha field, with a 0.09 ha farm pond (which stored excess water from the wet season) 28-37 per cent of seasonal rainfall was available as surface runoff from a microcatchment (0.66 ha growing groundnut) for collection in the pond and is sufficient to prevent drought stress (Rathore *et al.*, 1996).

Leaf thermocouple hygrometers and specially fabricated stem thermocouple hygrometers were evaluated by Pallas (1978) in groundnut plants under well-watered drought conditions in a growth chamber. When soil-water stress was low and plant-water movement was near steady state, the 2 sensors gave similar water potential values. When soil-water stresses were imposed or when plant process varied cyclically (*e.g.* photosynthesis, transpiration), stem hygrometers sensed dynamic changes in the plant's water potential more consistently than did leaf hygrometers placed in leaves with intact cuticles. Thus, both the stem and leaf hygrometers may be useful for sensing water potential changes of groundnuts under field conditions Rosario and Fajardo (1988) compared 4 high-yielding, 1 low-yielding and 5 intermediate-yielding groundnut cultivars in pot at field water capacity throughout or at 50 per cent field water capacity 14-80 DAS and then watered to FC for 1 week and again subjected to water stress until harvest, significant interactions between cultivar and water stress on stomatal resistance, leaf water potential and root DW were observed and WUE decreased under water stress in all cultivars with a marked decrease in cv. TMV 2 (intermediate yielding) and EG Bunch (low yielding).

At wilting point the transpiration rate in groundnut decreased to 67 per cent. The diffusive resistance increased during drought and after withholding the irrigation for 2-6 days, the RWC was only 30-38 per cent of that at full turgidity. The leaf water potential ( $\psi_l$ ) is an important parameter, which is measured through psychometric in laboratory; however in field the pressure chamber technique and hydraulic press methods are most common. Saturation deficit (SD) is an important agroclimatic factor controlling the potential evaporation. The groundnut crops are often irrigated or grown on stored moisture during the post-rainy season when SD exceeds 3-4 kPa. This SD has a major effect on the water-use rate and the growth of groundnut as the WUE is inversely proportional to SD. SD more than 2.5 kPa accelerated the depletion of soil moisture reserves and greatly reduces LAI by lowering the turgor potential of expanding leaves. Because expanding leaves are more sensitive to moisture deficit than pods, the partitioning of dry matter is likely to be affected by SD.

The response of leaf area expansion to atmospheric saturation deficit (SD) and soil moisture deficit when examined in terms of leaf water potential and turgor potential by growing groundnut plant at different levels of SD and control with soil kept irrigated to FC, the SD accelerated the depletion of soil moisture reserves in the unirrigated stands and greatly reduced LAI, leaf number/plant and leaf size, but the effect on leaf size was greater than number. SD had less effect than soil water deficit on leaf production. Turgor potential and leaf extension rate were both reduced at high SD and leaf extension rate was linearly related to turgor potential between 0900 and 1600 h. However, leaf extension rate and turgor potential were poorly correlated between 0400 and 0700 h in the driest treatment (Ong *et al.*, 1985).

Mature leaves of well watered field grown groundnut cv. Florunner and Early Bunch were detached and changes in leaf water potential of these leaves and leaves of 10 genotypes subjected to water stress in the field when compared, detached leaves turgor potential (TP) decreased to zero at -1.2 to -1.3 MPa leaf water potential ( $\psi_l$ ) and 87 per cent RWC for both cv. Small errors in leaf solute potential (LSP) determined by thermocouple psychrometry, resulted in artefactual negative TP values. In the field tests zero TP occurred at LWP of -1.6 MPa indicating that water relations of groundnut were similar to other crops with no unique drought resistance mechanism (Bennett *et al.*, 1981). In pots, the groundnut cvs. ICGS 1, ICGS 5, ICGS 11, ICGS 44, ICGS 76, ICG (FDRS) 55 and Girnar 1 water stressed at the flowering stage for 4 d, increased stomatal diffusive resistance and proline content and decreased transpiration rate, total chlorophyll, carotenoids and polyphenol contents. The better performance of cv. ICGS 11, ICGS 44 and Girnar 1 under water stress was related to good stomatal conductance and increased proline level for osmotic adjustment (Patil and Patil, 1993). The groundnut leaves entered permanent wilting status at <55 per cent RWC (Nwalozie and Annerose, 1996).

The pressure chamber for measuring leaf water potential in groundnuts when compared with the thermocouple psychrometer in field at Kingaroy on groundnut cv. Q18801, Red Spanish and McCubbin, the pressure chamber over-estimated leaf water potential by an average of 0.4 MPa over the range -0.5 to -5.0 MPa. The study concluded that the pressure chamber technique could be appropriate in comparative studies of groundnut water stress, however, for absolute measurements, as in the calculation of

leaf turgor potential, either a correction factor be applied or, preferably, the thermocouple psychrometer technique used (Wright *et al.*, 1988). The RWC of the leaf (97-81 per cent) and water potential of the leaf (-10 to -38 bar) declined with a decrease in soil-water potential from -0.5 to -20 bar. The RWC of the leaf did not recover to its original value on re-watering after severe stress. Cv. TG 17 tolerated water stress better than cv. GAUG 1 (Patel *et al.*, 1983).

The temperature and water stress effect on plant water status, stomatal conductance and water use in groundnut cv. Robut 33-1 studied by Black *et al.* (1985) in controlled environment greenhouses at 25, 28 or 31°C at two treatment (irrigation to half of the stand whenever soil water potential at 10 cm reached -20 kPa and the other half received no further irrigation after sowing, when the soil profile was at FC), the Leaf water potential (LWP), turgor potential (TP) and stomatal conductance (SC) were reduced in unirrigated plants at 29 DAS, when LAI was still below 0.5; SC was more strongly affected than water status. These differences persisted throughout the season as stress increased but SC was poorly correlated with LWP and TP. The decreases in SC and LAI reduced canopy conductance by up to 40 per cent. The conservative influence of decreased SC in unirrigated plants was negated by increases in leaf-to-air vapour pressure difference caused by their higher leaf temp. Transpiration rates were similar in both treatments and the lower total water use of the unirrigated stand resulted entirely from its smaller LAI. Unirrigated plants made less vegetative growth but produced more pegs and pods, although impaired pod-filling reduced pod yields by approx. 35 per cent (Black *et al.*, 1985).

Extensive root system combined with the ability to extract moisture under soil moisture deficits can delay dehydration and prolong the effective production period. Both of these can be evaluated at seedling stages in breeding lines. Matthews *et al.* (1988a) observed that the genotypes with limited irrigation, in central India, transpired similar total amount of water (220-226 mm) over the seasons, but produced different amounts of shoot dry matter varying from 390-490 g m<sup>2</sup>. Joshi *et al.* (1988) identified GG 2 as drought tolerant variety and JL 24 as sensitive cultivar. The lower leaf water potential and diffusive resistance (DR), higher transpiration rate and quick recovery of stomatal activity after relief of the stress and maintenance of low leaf water potential even at high RWC were the main reason for resistance in GG 2. Moderate water deficit at pre-flowering phase (without irrigation from 21 to 50 DAS) showed higher mean stomatal conductance, crop growth rate, pod growth rate, and yield than the control getting regular irrigation alfisol and vertisol.

Nageswara Rao *et al.* (1988) reported that applying two irrigations at 11 and 21 DAS followed by withholding irrigation for 30 days (up to 50 DAS) and again irrigation (at 50 per cent FC) at 10 days intervals showed the mean stomatal conductance 8.3-11.5 mm s<sup>-1</sup>, CGR 12.2-13.1 g m<sup>-2</sup> day<sup>-1</sup>, pod growth rate (PGR) 9-9.9 g m<sup>-2</sup> day<sup>-1</sup>, partitioning factor (PF) 74-76 per cent and pod yield 5.3-5.5 t ha<sup>-1</sup> in Robut 33-1 groundnut, however, the crop irrigated to 50 per cent FC at 10 days intervals showed the stomatal conductance 6.9-10.4 mm s<sup>-1</sup>, CGR 8.8-13.5 g m<sup>2</sup> day<sup>-1</sup>, PGR 6.4-10.2 g m<sup>2</sup> day<sup>-1</sup>, PF 73-75 per cent and pod yield 4.6-4.7 t ha<sup>-1</sup>. The responses of crops to drought stress under five farming systems in China reported that the differences in water potentials between the air and crop leaves were >100 times higher than those between

crop leaves and soil in the surface 10 cm layer and the differences between the latter were also >100 times higher than those between soils in the 10 cm and 70 cm layers (Zhang *et al.*, 1999). However, the differences in water potentials were lower with minimum tillage and narrow ridge tillage than with conventional tillage and wide ridge tillage respectively, indicating the serious water stress in the former treatments. The diurnal variation of water potentials in the soil-plant-atmosphere continuum indicated that groundnut is more tolerant of drought than soyabean and maize, leaf water potential decreased with the increase in soil water potential and its relationship could be expressed by binomial equations. With ridge tillage, leaf water potential was more related to the water potential of the deeper soil layers than to that of the soil surface under minimum tillage. Seasonal drought in the region is caused by combined water stress and high temperature, water potentials of soils and leaves increased with the increase in soil and air temperatures, respectively and the effect of temperature on water potentials of soils and leaves was influenced by farming practices and crop communities (Zhang *et al.*, 1999).

Effects of 5 drought (Early, middle and late drought periods of short duration of 35 days and extended early and midseason droughts of 70 days) imposed by withholding irrigation studied on Tifton loamy sand measuring the yield, percentage sound mature kernels (SMK), germination, leaf water potential and leaf diffusion resistance; drought progressively decreased yields as duration and lateness of occurrence in the season increased (Pallas *et al.*, 1979). In maize, groundnut and pearl millet, the water stress and aging of leaves within various canopies when studied after withholding irrigation for 7 d, the leaf temp., transpiration and PAR decreased with leaf aging, while diffusive resistance increased with aging, shading and water stress. Leaf temp., diffusive resistance and PAR of the crops were in the order: groundnuts < maize < pearl millet (Golakiya, 1989). In pot, groundnut cvs. Dh 330 and TMV 2 subjected to water stress at flower initiation (30 DAS), peg formation (40 DAS) or pod formation (70 DAS) by withholding water for one week, the leaf diffusive resistance and proline accumulation were highest and transpiration rate lowest with water stress at 70 DAS and cv. Dh330 was more tolerant to water stress as it had higher leaf diffusive resistance, lower transpiration rate and greater proline accumulation than TMV 2 (Koti *et al.*, 1994).

In Perkins, Oklahoma, irrigation at 5.5 cm/week or no irrigation (except rainwater) affected the leaf relative water content (LRWC) of groundnut cvs. Comet and Florunner grown on a Teller loam soil at soil relative water content (SRWC) above 50 per cent, the mean LRWC was about 85 per cent, and was affected more by evaporative demand than by SRWC. Below 50 per cent SRWC, LRWC was highly correlated with SRWC. The predicted SRWC when turgor pressure potentials approached zero was about 45 per cent. This SRWC threshold occurred under rainfed conditions in the 3 years study at 59, 56 and 64 DAP during flowering and pod formation. Thus, the SRWC vs. soil water pressure potential curve of Teller soil may be useful for predicting limiting levels of soil water for groundnut and that limiting levels of soil water may occur well above the classically defined lower limit of soil water availability (Erickson *et al.*, 1991).

### 3.6. Photosynthesis and Fluorescence

The plant water and soil moisture stress when investigated on photosynthesis, stomatal aperture and transpiration in groundnut, maximum photosynthesis occurred at a soil moisture content (MC) of 50-60 per cent (of the maximum water-holding capacity) and at a leaf DPD (diffusion pressure deficit) of 1-1.5 atm. Photosynthesis of groundnut was adversely affected by a high soil MC. The photosynthesis, stomatal aperture and transpiration were all affected by low soil MC, before the leaves showed visible signs of wilting and hence stomatal aperture may be used as a physiological indicator of necessity of irrigation (Chen and Chang, 1972). Bhagsari *et al.* (1976) reported that in groundnut cvs. Florunner and Tift-8, the relation between net photosynthesis and RWC measured in single leaf during a 5 to 6 day period without water was similar, diffusive resistance was 0.5-2.5 s/cm in control plants, 30-35 s/cm in stressed plants and 18-20 s/cm in stressed groundnut cv. Florunner, P.I. 149268 and the wild *Arachis monticola*. The water potential of immature pods was equal to or slightly higher than that of leaves at the end of the outdoor trial. There were no differences among cultivars in response to water stress and it is concluded that net photosynthesis in groundnut is controlled by water stress in a manner quantitatively similar to that in other crop species (Bhagsari *et al.*, 1976).

Wang *et al.* (1995) in a field at Laixi, China, two high-yielding groundnut cultivars (Luhua 11 and Haihua 1) characterized by few branches, medium duration of growth, and large pods studied for the physiological characteristics related to their canopy morphology such as light distribution through the canopy, light interception rate (LIR) at different stages of plant development, diurnal and seasonal variations in photosynthesis, dark respiration, and the effects of water deficiencies and listed Physiological indices for the groundnut canopy that would ensure yield of 7.0-7.5 t ha<sup>-1</sup>. The major area of photosynthesis was the upper one-third of the canopy which received four-fifths of the solar radiation and contained about half of the total leaf area. The LIR of the canopy remained low (50 per cent of solar radiation reached the ground) until the flowering-pegging stage but rose to a peak which was maintained until the early-mid pod-filling stage. The diurnal variations in photosynthesis on a clear day showed a peak between 1100 and 1300 h. No sign of 'noon rest' or light saturation was evident under natural conditions so the dominant factor was intensity of solar radiation. Dark respiration was maximum at 1100-1500 h and minimum at 0300-0500 h, and was strongly dependent on air temperature. Over the growing season the net photosynthetic rate increased slowly during the seedling stage and accelerated from the flowering-pegging stage until midpod formation when it reached a peak. Photosynthesis was more sensitive to water deficiency than dark respiration. Physiological indices for the groundnut canopy that would ensure yields of 7.0-7.5 t ha<sup>-1</sup> are listed (Wang *et al.*, 1995).

The effect of water deficit on nodulation, N<sub>2</sub>-fixation, photosynthesis, total soluble sugars and leghaemoglobin in nodules was investigated where Nitrogenase activity completely ceased in groundnuts at -1.7 MPa. With increasing water stress, the acetylene reduction activity decreased gradually in groundnuts. Nodule FW declined in groundnuts when leaf water potential decreased by 1.0 MPa, but no nodule shedding was noticed even at a higher stress level in groundnuts. Photosynthesis

and stomatal conductance were more stable in groundnuts than in *V. unguiculata* under water stress. There was a sharp increase in total soluble sugar and leghaemoglobin in the nodules of groundnuts with water stress, but no definite trend in *V. unguiculata* (Venkateswarlu *et al.*, 1989).

Matsunami and Kokubun, (2003) studied the specific differences in the photosynthetic responses of four legume crops to daily fluctuations of evaporative demand and to identify physiological attributes responsible for the differences, soyabean (cv. Enrei), adzuki bean (cv. Dainagon), cowpea (cv. Kuromidori) and groundnut (cv. Chibahandachi) in field of Tohoku University, Japan, and apparent leaf photosynthetic rate (AP) and gas exchange parameters and water potential and transpiration rate were measured at midday where leaf-to-air vapour pressure deficit (VPD<sub>la</sub>) varied from 1.72 - 3.44 kPa the four species responded differently, the AP of soyabean and that of adzuki bean decreased with increasing VPD<sub>la</sub> whereas the activities of cowpea and groundnut were greatest at VPD<sub>la</sub> around 2.53 kPa. The leaf water potentials of soyabean, adzuki bean and cowpea reached their lowest at VPD<sub>la</sub> around 2.53 kPa, while that of groundnut was fairly constant over the VPD<sub>la</sub> range of 1.72 to 3.44 kPa. The transpiration rates of soyabean, adzuki bean and cowpea were greatest at VPD<sub>la</sub> ~2.53 kPa and decreased beyond that range of VPD<sub>la</sub>, while groundnut transpired actively with increasing VPD<sub>la</sub>. AP of soyabean was correlated with leaf water potential, whereas that of cowpea and groundnut was correlated with transpiration rate. With respect to water relations, groundnut was the most tolerant of increasing VPD<sub>la</sub> among the four species tested, presumably because it maintained higher water potential and transpiration rate than the other species under the condition of high VPD<sub>la</sub>.

Clifford *et al.* (1993) reported that the primary effects of elevated CO<sub>2</sub> on growth and yield of groundnut stands were mediated by an increase in the conversion coefficient for intercepted radiation and the prolonged maintenance of higher leaf water potentials during drought stress. Groundnut cv. Kadiri3 grown in controlled-environment greenhouses at 28 °C (±5°) under 2 levels of atmospheric CO<sub>2</sub> (350 or 700 ppmv) and 2 levels of soil moisture (irrigated weekly or no water from 35 d after sowing) where elevated CO<sub>2</sub> increased the maximum rate of net photosynthesis by up to 40 per cent with an increase in conversion coefficient for intercepted radiation of 30 per cent (1.66 - 2.16 g MJ<sup>-1</sup>) in well-irrigated conditions, and 94 per cent (0.64 - 1.24 g MJ<sup>-1</sup>) on a drying soil profile. Elevated CO<sub>2</sub> increased DM accumulation by 16 per cent (from 13.79 to 16.03 t ha<sup>-1</sup>) and pod yield by 25 per cent (from 2.7 to 3.4 t ha<sup>-1</sup>), but the HI was not affected. The beneficial effects of elevated CO<sub>2</sub> were enhanced under severe water stress; DM production increased by 112 per cent (from 4.13 to 8.87 t ha<sup>-1</sup>), and a pod yield of 1.34 t ha<sup>-1</sup> was obtained in elevated CO<sub>2</sub>, whereas comparable plots at 350 ppmv CO<sub>2</sub> only yielded 0.22 t ha<sup>-1</sup>. There was a corresponding decrease in HI from 0.15 to 0.05. Following the withholding of irrigation, plants growing on a stored soil water profile in elevated CO<sub>2</sub> could maintain significantly less negative leaf water potentials for the remainder of the season than comparable plants grown in ambient CO<sub>2</sub>, allowing prolonged plant activity during drought. On a drying soil profile, allocation in plants grown in 350 ppmv CO<sub>2</sub> changed in favour of root



development far earlier in the season than plants grown at 700 ppmv CO<sub>2</sub>, indicating that severe water stress was reached earlier at 350 ppmv CO<sub>2</sub> (Clifford *et al.*, 1993).

Subramanian and Maheswari, (1990) reported that groundnut plants adapt to water stress by slowing down tissue dehydration. Groundnut plants, subjected to water stress at flowering by withholding irrigation for 4 d and leaf water potential ( $\psi_1$ ), transpiration rate, stomatal conductance and photosynthetic rate measured daily in the morning until the young leaflets folded vertically where LWP, transpiration rate and photosynthetic rate decreased progressively with increasing duration of water stress, indicating that plants under mild stress postpone tissue dehydration, stomatal conductance decreased almost steadily during the stress period indicating that this was more sensitive than water loss during the initial stress period. Sharma *et al.* (1993) reported that groundnuts cv. M 13 grown in pots by withholding water for 1-4 d at flowering (30 DAS), reduced photosynthetic rate, leaf water potential and transpiration rate, water stress was mild in the 1<sup>st</sup> and 2<sup>nd</sup> day, but stomatal conductance decreased progressively with prolonged water stress. Photosynthetic rate was 0.30 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> after 4 d of stress compared with 0.80 mg in control plants. Phosphoenolpyruvate carboxylase activity progressively increased with stress whereas the activities of RuBP carboxylase and NADP-glyceraldehyde-3-phosphate dehydrogenase decreased gradually (Sharma *et al.*, 1993).

During rainy seasons groundnut cv. JL24 (recommended for irrigated areas), TMV 2 and Kadiri 3 (recommended for dryland areas) grown on red sandy loam soil (Alfisol) under irrigated or dryland conditions, seasonal average photosynthetic rate, transpiration rate, stomatal conductance and leaf water potential were lower and canopy temperature higher under dryland than irrigated conditions due to drought. TMV 2 and Kadiri 3 stomatal conductance was lower by 25 per cent and photosynthesis by 22 per cent, however, transpiration rate was lower by only 9 per cent. At peak flowering JL 24 had significantly higher canopy temperature than TMV 2 and Kadiri 3. Thus measurements of integrated physiological processes, rather than of instantaneous rates of assimilation and water loss, are likely to reveal a basis for cultivar differences in water limited environments (Subramanian *et al.*, 1993).

The response of photosynthesis to soil moisture availability is significantly faster in the tolerant groundnut genotypes compared to susceptible plants, and this appears to be, in part, caused by better stomatal control. Kameshwara Rao *et al.* (2009) suggested that light-saturated photosynthesis (A) was similar in the tolerant (COC 041) and susceptible (COC 166) genotypes of groundnut before water stress was applied (0 d) and at the end of the stress period (7 d), but (A) was higher in the susceptible genotype during stress exposure (3 d) because of higher stomatal conductance. On the second day after re-watering, A and gs were higher in the tolerant genotype reacting faster recovery from stress, but 7 d after re-watering both genotypes had fully recovered. Instantaneous leaf-level WUE (A/gs; WUE) was higher in the tolerant genotype prior to and during the onset of water deficit because of lower gs. However, upon return to saturated soil moisture conditions, assimilation rates and stomatal conductance increased rapidly (within 48 h), and WUE was lower in the tolerant genotype compared to the susceptible genotype. Although the susceptible genotype showed a slower recovery following the stress treatment, both genotypes recovered to pre-stress

levels of photosynthesis 7 d after re-watering. As a consequence of water stress, the photosynthetic machinery may be reversibly and partially de-activated to reduce detrimental loss of water, but may be rapidly activated upon re-watering. This is an essential trait for production agriculture where plants are continually exposed to intermittent irrigation events in both rain-fed and irrigated conditions. In tolerant groundnut genotype (COC 041), a 30 per cent decrease in irrigation levels in the field only reduced yield by 15–20 per cent compared with 90 per cent in the susceptible genotype, which is a substantial difference in real-world application. This yield response appears to be correlated with a rapid down regulation of photosynthesis via stomatal closure and decrease in photosynthetic machinery which could minimize water loss from the plant and prevent cellular damage. Additionally, higher epicuticular wax may minimize additional water loss from the tolerant genotype. Upon re-irrigation, the tolerant genotype rapidly regains a significant percentage of its non-stressed photosynthetic capacity. Interestingly, the tolerant genotypes fail to exhibit up regulation of many proteins known to be responsive to stress, suggesting that under the similar levels of available soil moisture, the tolerant genotype does not experience the same level of stress as experienced by the susceptible genotype. Although both tolerant and susceptible plants recover full photosynthetic capacity within 1 week of re-irrigation, it is perhaps the recovery phase and potential energy costs associated with cellular repair that ultimately have an impact on significantly reducing yield in the susceptible genotype (Kameswara Rao, 2009).

To study the effect of drought on the mechanisms of energy dissipation, Lauriano (2006) conducted a trial using two-month-old *Arachis hypogaea* cvs. 57-422, 73-30, and GC 8-35 submitted to three treatments: control (C), mild water stress ( $S_1$ ), and severe water stress ( $S_2$ ). Photosynthetic performance was evaluated as the Hill and Mehler reactions. These activities were correlated with the contents of the low and high potential forms of cytochrome (cyt) b559, plastoquinone, cyt b563, and cyt f. Under mild water stress the regulatory mechanism at the antennae level was effective for 57-422 and GC 8-35, while in the cv. 73-30 an overcharge of photosynthetic apparatus occurred. Relative to this cv. under  $S_1$  the stability of carotene and the dissipative cycle around photosystem (PS) II became an important factor for the effective protection of the PSII reaction centres. The cyclic electron flow around PS I was important for energy dissipation under  $S_1$  only for the cvs. 57-422 and 73-30.

Lauriano (2004) measured the photosynthetic response of three *Arachis hypogaea* L. cultivars (57-422, 73-30, and GC 8-35) grown for two months under water available conditions, severe water stress, and 24, 72, and 93 h following re-watering. At the end of the drying cycle, all the cultivars reached dehydration, relative water content (RWC) ranging between 40 and 50 per cent. During dehydration, leaf stomatal conductance (gs), transpiration rate (E), and net photosynthetic rate (PN) decreased more in cvs. 57-422 and GC 8-35 than in 73-30. Instantaneous water use efficiency (WUEi) and photosynthetic capacity (Pmax) decreased mostly in cv. GC 8-35. Except in cv. GC 8-35, the activity of photosystem I (PS I) was only slightly affected. PSII and ribulose - 1, 5-bisphosphate carboxylase/oxygenase (RuBPCO) were the main targets of water stress. After re-watering, cvs. 73-30 and GC 8-35 rapidly regained gs, E, and PN

activities. Twenty-four hours after re-watering, the electron transport rates and RuBPCO activity strongly increased. PN and Pmax fully recovered later.

Measurement of chlorophyll (Chl) fluorescence constitutes one of the oldest approaches to investigate photosynthesis, the first Chl fluorescence experiments being reported more than 70 years ago. Monitoring fluorescence induction (FI) has become a widespread method for probing photosystem II (PSII), mostly because it is non-invasive, easy, fast, and reliable, and requires relatively inexpensive equipment. When dark-adapted photosynthetic samples are excited with actinic light, FI is characterized by the initial fluorescence level ( $F_0$  or  $O$ ), which represents excitation energy dissipated as photons before it reaches open reaction centres, and a subsequent rise from  $F_0$  to maximal level ( $F_m$  or  $P$ ), related to a series of successive events that lead to the progressive reduction of the quinone molecules located on the acceptor side of PSII.

Kameshwara Rao *et al.* (2009) evaluated 17 genotypes from the US groundnut mini-core collection and three check cultivars using the chlorophyll fluorescence screening technique following imposition of water-deficit stress. Of these 20 genotypes, we identified as stress-tolerant (COC 041, COC 384, COC 249, COC 149, TMV 2) and we stress-susceptible (COC 166, COC 227, COC 068, Tamrun OL 02, ICGS 76) genotypes based on observations of chlorophyll fluorescence yield, whole-plant WUE (mg mass produced per g of water used, and specific leaf area. Tolerant genotypes were characterized by smaller percentage changes in chlorophyll fluorescence yield during water-deficit stress, higher WUE during well-watered and deficit stress conditions and slightly higher SLA, compared with susceptible genotypes. The most tolerant genotype (COC 041) exhibited a similar decline in fluorescence yield over time in both water-stressed and well-watered plants. In contrast, the most susceptible genotype (COC 166) exhibited a marginal decline in fluorescence yield in the water-stressed plants after 72 h of incubation.

In groundnut leaf dehydration enhanced variable fluorescence yield immediately and the model of pattern alteration of fluorescence curves by dehydration included three stages: an increase of variable fluorescence and the steady state of fluorescence, the formation of a fluorescence "plateau" and an eventual decline of fluorescence. The maximum yield of fluorescence was usually reached as the plateau appeared. The water content at which point the plateau was completely formed was critical and may be species/genotype dependent. Leaf rehydration could restore transient fluorescence before this point was reached. The dehydration-rehydration cycle experiments indicated that the block on the photoreducing side of PSII was reversible, whereas the change on the water splitting side was irreversible. Comparing superoxide dismutase (SOD) levels in leaves of different plants, the wild groundnuts had more SOD than a cultivated groundnut based on leaf FW. Both cyanide-sensitive and insensitive SOD isoenzymes were found in leaves of wild groundnuts. In contrast, the isoenzymes in leaves of cultivated groundnuts were cyanide-sensitive and mainly chloroplastic isoenzymes. Paraquat reduced SOD activity markedly in groundnut leaves (Wu, 1987).

Clavel *et al.* (2006) obtained genotypic and treatments responses in groundnut on some of the fluorescence parameters, in particular the structure-function-index

values that traduce the status of photochemical apparatus. The technique of chlorophyll uorescence, as it is rapid, sensitive and non-destructive, could therefore become a useful method for determining variations in tolerance of the photosynthetic apparatus in breeding for resistance to drought. Nevertheless, the role and value of the fluorimetric responses for maintaining yield under drought needs to be clarify due to difference existing in groundnut drought adaptation strategies. Future selection schemes for improvement of drought adaptation in the cultivated groundnut species are therefore possible by using uorescence parameters in association with yield-based studies in the eld. Thus Chlorophyll a fluorescence is a highly versatile tool, for researchers studying photosynthesis as well as for those working in broader fields related to physiology of plants.

Kalariya *et al.* (2012b) studied the chlorophyll fluorescence and net photosynthesis under water deficit conditions in six groundnut (*Arachis hypogaea* L.) cultivars by withholding irrigation from 31 to 60 DAS (between beginning bloom to beginning seed) and 60 to 87 DAS (beginning seed to beginning maturity). The soil moisture content was 17 per cent and 18 per cent at 0-15 and 15-30 cm soil depth in well watered plots which decreased to 9 per cent and 10 per cent respectively in water deficit plots during on 60 DAS. A similar trend was followed during 60-87 DAS also. The RWC of groundnut leaves decreased from 92 in control to 88 under water deficit condition at 60 DAS with the least decrease in ICGS 44. The water deficit stress has decreased maximum efficiency of PS II ( $F_v/F_m$ ) and proportion of absorbed energy utilised for photochemistry ( $\dot{O}PS II$ ), net photosynthesis rate and thereby linear electron transport rate] but, increased minimum fluorescence ( $F_0$ ) and non-photochemical quenching ( $NPQ$ ) 60 and 87 DAS (Kalariya *et al.*, 2012a). Water deficit stress increased minimum fluorescence ( $F_0$ ) and non-photochemical quenching ( $NPQ$ ) but, decreased maximum efficiency of PS II ( $F_v/F_m$ ) and proportion of absorbed energy utilised for photochemistry ( $\dot{O}PS II$ ) at 60 DAS due to water deficit stress imposed 30-60 DAS in groundnut (Kalariya *et al.*, 2012b).

The water deficit condition during 30-60 DAS has significantly increased  $F_0$  and  $NPQ$  but decreased the maximum quantum yield of PS II ( $F_v/F_m$ ) from 0.81 in control to 0.77 at 60 DAS which was again resumed to 0.80 after 48 hours of withdrawal of stress. The rate of photosynthesis which was 29 and 36  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in well irrigated plots decreased to 26 and 28  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with a deduction of 11 and 30 per cent at 60 DAS and 87 DAS, respectively. Variety TAG 24 showed better stress recovering capacity with high photosynthesis under both control as well as water deficit condition whereas, data on chlorophyll fluorescence parameters showed that variety ICGS 44 was least affected to damage via photoinhibitory action (Kalariya *et al.*, 2013).

### 3.7. Translocation

Soil moisture deficits imposed between sowing and pod initiation or between pod initiation and final harvest of groundnuts by regulating irrigation and  $^{14}\text{CO}_2$  on 5-6 occasions between 50-97 DAS were studied in a controlled environment by Stirling *et al.* (1989). The study reveals that leaves were the primary sites of  $^{14}\text{CO}_2$  fixation, though their contribution generally declined late in the season; whereas fixation by stems was initially low but increased sharply when stress was released in the late-

irrigated stands.  $^{14}\text{C}$ -fixation by stem apices and pegs also rose sharply following irrigation of the late-stressed stands. Leaves were the primary source of assimilates, but translocation tended to decrease as the season progressed, even in the late-irrigated stands. Stems were initially the major sinks, but their sink activity disappeared almost completely when stress was released in the late-irrigated stands. Assimilate import by stem apices declined progressively and pod sink activity was negligible in the late-stressed stand, but both increased markedly when early-season stress was released. Leaf water status showed marked diurnal variation; pegs showed less variation and maintained much higher turgor levels, largely because of their lower solute potentials. Marked osmotic adjustment occurred in expanding but not in mature leaves, allowing them to maintain higher turgor levels during periods of severe stress. This adjustment was rapidly lost when stress was released. The observed changes in assimilate production and partitioning preceded detectable changes in bulk turgor levels (Stirling *et al.*, 1989).

Clavel *et al.* (2005) assessed the field productivity of four Sahelian groundnut cvs during three crop seasons in Bambey (Senegal) and same cvs grown in rhizotrons were subjected to early drought stress and to a desiccation test to assess cell membrane tolerance, where differences were found between cultivars with respect to pod yield, biomass production, WUE, stomatal regulation and cell membrane tolerance and to cope with water deficit two strategies were identified. The first was characterised by rapid water loss, late stomatal closure and low cell membrane damage during drought which were found in the semi-late Virginia cv 57-422 and, into a lesser extent, in the early Spanish cv Fleur 11. The biomass production was boosted in both the cvs under favourable conditions in rhizotrons but the semi-late cv had poor pod yield under end-of-season water deficit conditions. The second strategy involved opposite characters, leading to the maintenance of a high water status, resulting in lower photosynthesis and yield. This characterised the early Spanish cv 73-30, and also, to some extent, the early Spanish cv 55-437. Earliness associated with high WUE, stomatal conductance and cell membrane tolerance, were the main traits of Fleur 11, a cv derived from a Virginia x Spanish cross, which was able to maintain acceptable yield under varying drought patterns in the field. These traits, as they were detectable at an early stage, could therefore be efficiently integrated in groundnut breeding programmes for drought adaptation (Clavel *et al.*, 2005).

The environmental factors influencing pod yield in groundnuts operated mainly through their effect on the timing of pod initiation and the size of reproductive sink, as defined by the number of pods set (Stirling, 1989). During the post-rainy season, the effect of artificial (bamboo screens) or the onset of rapid pod growth to final harvest and natural (sorghum) shading on growth and development of groundnuts when examined in terms of the associated changes in leaf and soil temperature and plant water status, the artificial shading with bamboo screens providing approximately 45 per cent shade substantially reduced leaf and soil temperature relative to the crop grown alone, this had little effect on plant morphology and DW at final harvest (Stirling, 1989). Root respiration at 30 d after sowing (DAS) was increased under water-stressed conditions. Yield was negatively correlated with root respiration 30 and 60 DAS. Cv. JL 24 was the most tolerant of water stress, with a yield reduction

in stressed conditions of 32.1 per cent compared with an average of 46.7 per cent, and a 66.9 per cent yield reduction in the most susceptible cultivar (TAG 24) (Dhopte *et al.*, 1992).

### 3.8. Biochemical Parameters

Dwivedi *et al.* (1986) described a biochemical test for prediction of drought resistance in groundnut cultivars based on chelation of the youngest fully opened leaves with 0.1 M EDTA and extraction of organic substances and osmotically-active compounds; the degree of decrease in the pH of EDTA extract of leaves is related to drought resistance and the cultivars showing <2.8 per cent decrease in the pH of EDTA extract of leaves at -10 bar water stress are considered as drought resistance. Drought resistance in 22 cvs. was determined using this test and examined in relation to stomatal resistance, transpiration rate, saturated water deficit, pH water deficit, pH water deficit index and decrease in pod yield under water stress (Dwivedi *et al.*, 1986). Water stress at 2-6 atm decreased protein contents and increased amino acid and proline contents in leaves of 15 d old groundnut seedlings, decreased peroxidase and nitrate reductase activities and increased ribonuclease activity and proline content and ribonuclease activity could be used as indication of water stress in groundnut seedlings (Sharma *et al.*, 1990).

The epicuticular wax load (EWL) on leaves reduces transpiration and improves crop WUE and, genotypic differences were observed in EWL of 12 genotypes grown in the rainy season at 45 DAS by Samdur *et al.* (2003) and the values of EWL ranged from 0.91 mg dm<sup>-2</sup> in Chico to 1.74 mg dm<sup>-2</sup> in PBS 11049, with a mean of 1.27 mg dm<sup>-2</sup>. The mean values were 1.10, 1.58, 2.05 mg dm<sup>-2</sup> at 45, 75, and 95 DAS, respectively. In both dry seasons, genotypic differences were found in the EWL and effect of various moisture deficit treatments and their interactions with the genotypes were observed with values ranged from 0.653 to 2.878 mg dm<sup>-2</sup>. The highest EWL was found in PBS 11049 (2.24 mg dm<sup>-2</sup>). The EWL increased with age of the crop, with greater increase under moisture deficit stress. Thus the genotypic differences exist in EWL of groundnut and this EWL increases with increased crop age and more pronounced under protracted moisture deficit stress (Samdur *et al.*, 2003). The methyl jasmonate (0-125 mg/litre) application in groundnut grown in nutrient solution and treated at the 3- or 4-leaf stage with polyethylene glycol where methyl jasmonate decreased stem height, leaf area and transpiration rate, and increased leaf thickness, the size of water storage cells in leaves, ABA and proline contents of leaves and peroxidase activity in stems. Methyl jasmonate decreases water loss, and may help groundnut seedlings adapt to drought (RuiChiand HuangQing, 1995).

In response to environmental changes in temperature, oxygen or water levels stress proteins occur in groundnut seeds during maturation and curing because these processes are known to be associated with water deficit and anaerobic metabolism in seeds and to test this hypothesis, a polyclonal antibody against dehydrin, a plant stress protein, was used by Chung *et al.* (1998) and the immunoblot analyses showed that a number of dehydrin-related stress proteins were detected in groundnut seeds of different maturity and curing stages, of these, only two were induced during seed curing and maturation. One (protein a) is potentially a groundnut

maturity marker because it was shown to occur only in uncured fully mature seeds. Immunoblot analyses of alcohol dehydrogenase (ADH), an enzyme known to be induced in mature groundnut seeds, showed that ADH was not recognized by the antibody. This suggests that ADH is probably not related to protein a or dehydrin (Chung *et al.*, 1998).

Groundnut cultivars grown at different water regimes (75, 50 and 25 per cent FC corresponding to mild, moderate and severe water stress, respectively) decreased leaf dry matter and relative water content with water stress in both cultivars, with K 134 being more tolerant compared to JL 24. The total leaf protein content decreased, whereas the free amino acid and protease activity increased with the increase in water stress. A 2-3 fold increase in proline content was recorded by K 134 and JL 24, respectively, in response to water stress. The better maintenance of RWC, dry matter accumulation, free amino acid and proline and protease activity of K 134 makes it a more drought-tolerant cultivar than JL 24 (Madhusudhan *et al.*, 2002). Generally 400-1000 mg proline m<sup>-2</sup> accumulated in vegetative parts. Accumulation of K<sup>+</sup> in leaf was identified as one of the good parameter for drought tolerance in groundnut (Arjunan *et al.*, 1988). The PP 333 (Paclobutrazol) caused the accumulation of indigenous ABA and the inhibition of GA biosynthesis in groundnut leaves and increases the drought resistance of groundnut seedlings (Ling and Rui-chi, 1988). Nautiyal, *et al.* (2001) reported the response of groundnut to various aspects of deficit irrigation practices during vegetative phase.

The mild and moderate drought (20 or 30 days) at different crop growth stages in groundnut cv. GG 2 withholding irrigation for 20 days, the total carbohydrate concentration and its fractions did not change except during the pod maturity stage where an increase was observed. After 30 days without irrigation, an increase in the total carbohydrate concentration and its fractions at all crop growth stages was observed. However, a significant reduction in the total carbohydrate and sugar contents (mg/kernel) was observed for both mild and moderate drought at any crop growth stage. Total lipid concentration in the kernel significantly decreased in response to drought for 20 or 30 days at different crop growth stages except for 30 days of drought at the pod maturation stage. The content of total lipid/kernel decreased at all crop growth stages. The proportions of non-polar and polar lipids and individual phospholipids were not influenced by drought (Kandoliya *et al.*, 2000). The benzyladenine soaking of seeds followed by PEG 6000 induced water deficit stress in leaf of 15 day old seedlings and among the groundnut cultivars GG 2, GG 3, GG 4, GG 5, GG 7 and J 11, the GG 2 showed highest RWC, greater accumulation of proline, ascorbic acid and reducing sugars whereas, cv. J 11 had the lowest RWC and showed lower proline and sugar (Dhruve and Vakharia, 2007). Increasing the level of PEG, simulated water stress showed reduction in RWC whereas the level of free amino acids, proline and sugars increased. Soaking of seeds in benzyladenine helped in amelioration of PEG simulated stress by maintaining higher RWC and maintaining adequate level of osmolytes (Dhruve and Vakharia, 2007).

Cell suspensions of the drought-susceptible groundnut cv. JL 24 and drought-resistant Kadiri 3 when inoculated into growth medium containing 2-15 per cent PEG, both cultivars showed rapid logarithmic growth up to 21 d and then reached a

plateau. Cell growth decreased significantly and linearly with increasing PEG concentration. With 15 per cent PEG cell DW after 21 d decreased by 51 per cent in Kadiri 3 and by 44 per cent in JL 24 compared with the control without PEG. When 25 d old whole plants were deprived of water for 6 d in the greenhouse, Kadiri3 maintained higher leaf water potential under water stress than JL 24. Proline accumulation was higher and tissue K content lower in cell culture and whole plants of JL 24 than in Kadiri 3. Since responses to stress in cell culture and in whole plants differ, the need is stressed for care in extrapolation of experimental data to predict field responses (Venkateswarlu *et al.*, 1993). The PEG stress tolerance in TMV 2 and JL 24 when compared at the fifth subculture stage on the stress to stress (selected) and control to stress (non-stress) medium showed further stress tolerance capacity of selected tissues in comparison with non-selected tissues. The JL 24 had a greater capacity to grow at all levels of stress (-0.6 to -0.1 MPa) and its tolerance was associated with higher values of pressure potential, amino acids and proline accumulation as compared to TMV 2 (Purushotham *et al.*, 1998).

### 3.9. Enzymes Activity

In greenhouse pot trials, 9 groundnut cultivars with different degrees of resistance to water stress, when subjected to water stress for 43 days from 15 DAS and then normal water supply, the water stress resistant cultivars showed similar patterns of peroxidase activity (Santos dos *et al.*, 1997). In 1-week-old groundnut seedlings water stress of -3 to -7 bar for 24 - 168 h, increased activities of both peroxidase and IAA oxidase with increase in the duration of water stress, increases in water stress levels showed smaller increase in the peroxidase activity but greater increase in the IAA oxidase activity, as compared with the control treatments (Mathews, 1988). Two groundnut cultivars (Jun 40 and GG 2) when compared for water deficit tolerance based on the RWC and membrane stability index. The results revealed that both these cultivars were tolerant. Cultivar Jun 40 accumulated superoxide ( $O_2^-$ ) radicals to a higher level and had higher activity of the scavenging enzyme superoxide dismutase. Increased activity of ascorbate peroxidase [L-ascorbate peroxidase] in the leaves of stressed plants of Jun 40 compared to GG 2 appeared to be responsible for the lower  $H_2O_2$  content. GG 2 showed less lipid peroxidation than Jun 40 under water deficit stress (Mittal *et al.*, 2006).

At USDA-ARS National Peanut Research Station Dawson, Georgia, the groundnuts cv. Florunner grown for 120 days, harvested at maturity, windrow dried for 4 days and sampled from day 4 further dried to 10 per cent moisture content and sorted by pod colour, shelled and the seeds stored at -80°C from which the enzyme extracts were prepared and colour assays developed. The study reveals that the activities of glycolytic enzymes (aldolase [fructose-bisphosphatealdolase], glyceraldehyde-3-phosphate dehydrogenase, pyruvate decarboxylase and alcohol dehydrogenase (ADH)) increased during groundnut maturation and curing, suggesting that these processes are associated with anaerobic conditions, furtete the enzyme activities were higher in cured groundnuts than in non-cured groundnuts, indicating anaerobic conditions were more severe in the former and the increase of ADH is primarily due to the increased activities of glycolytic enzymes preceding



ADH in the alcohol fermentation pathway (Chung *et al.*, 1997).

Common with other abiotic stresses, drought causes increased production of activated oxygen species (ROS) that inactivate enzymes and damage cellular components (Shao *et al.*, 2007, 2008). Oxidative stress occurs when the defence capacity of plants is broken by the formation of free radicals. Since water availability is usually the main factor affecting groundnut productivity in dry regions, strategies aiming at improving sustainable use of water and plant drought tolerance are urgent. Plants scavenge and dispose of these ROS by use of antioxidant defence systems present in several subcellular compartments. The enzymatic antioxidant system includes superoxide dismutase (SOD), peroxidase (PER), catalase (CAT), and the ascorbate and the glutathione cycle enzymes. The primary antioxidant metabolites are ascorbate,  $\alpha$ -tocopherol,  $\beta$ -carotene and glutathione. Superoxide dismutase accelerates the conversion of superoxide to hydrogen peroxide; catalase and peroxidase degrade hydrogen peroxide (Santos and Almeida, 2011). SOD constitutes the first line of defense via detoxification of superoxide radicals (Sairam *et al.*, 2000). The lower membrane stability index reflects the extent of lipid peroxidation, which in turn is a consequence of higher oxidative stress due to water stress conditions. Production of activated oxygen species (AOS) is one of the major secondary responses of stress.

Plants respond to various biotic and abiotic stresses threats by an efficient antioxidative system. The exogenous application (spraying on 20 day-old plants) of salicylic acid (0.014 and 0.028 per cent SA), *Acalypha fruticosa* chloroform leaf extract (1.0 per cent) and Neem Oil formulation (0.2, 0.5 and 1.0 per cent NO) on groundnut plants increased oxidative enzyme activities, total phenols and protein contents at 24, 48, 72 and 96 h after treatment with a quick response due to *A. fruticosa* which induced maximum enzyme activities (13.1 IU g<sup>-1</sup> FW POD and 0.48 IU g<sup>-1</sup> FW PPO, respectively, at 96 h after treatment). The total phenols, H<sub>2</sub>O<sub>2</sub> and protein contents were also high in *A. fruticosa* treated plants followed by those treated with NO (1 per cent) (War *et al.*, 2011). The *A. fruticosa* extract and neem oil influenced the metabolic system in plants and induced the oxidative response that could defend plants against a variety of stresses (War *et al.*, 2011).

The effects of drought stress induced from initial flowering of drought-susceptible and -tolerant groundnut cultivars when studied, the SOD activity decreased and the protein content increased during the early stress period. The SOD did not vary between the susceptible and tolerant cultivars, but the protein content in the tolerant cultivar was higher. With further exposure to drought, the SOD activity increased and the protein content decreased and at one stage, the SOD activity in the tolerant cultivar was greater than that in the susceptible cultivar, whereas the protein content did not vary significantly. An additional protein band was detected under drought stress, but no significant variation in protein components was recorded between the cultivars. The drought tolerant characteristics were the number of pods, yield per plant and seed weight in Yuhua 13 and FDRS10; SOD activity and protein content at the early stress period in Nankang Zhisizi; and SOD activity in Mashan Eryang. Under drought stress, water potential was higher in the dragon-type cultivars than in the other types

of cultivar (Jiang Hui Fang and Ren Xiao Ping, 2004).

A procedure was developed to screen groundnut plants for water stress tolerance based on in vitro growth and regeneration on a PEG containing medium and evaluated using 6 groundnut cultivars on media containing MS salts + B5 vitamins supplemented with 2 mg 2,4-D and 0.5 mg BAP [benzyladenine]/litre. PEG-4000 (5 per cent w/v) was incorporated into this media. Direct callusing of embryonic axes and regeneration on the PEG-containing medium was followed by rooting in non-stress media and plants regenerated on the stress medium exhibited higher osmolality than the control plants (regenerated on media without PEG-4000). The described procedure is a rapid, taking 3-4 months to complete, compared with protocols based on repeated passage of callus or suspension cultures in stress media which require almost one year (Venkateswarlu *et al.*, 1998).

Leaf discs taken from the seedlings of three groundnut cultivars differing in drought resistance when put in PEG-6000 solutions with osmotic potentials of -0.25, -0.75, -1.25 and -1.75 MPa and treated for 12 h. Water potential in the young leaves was shown to decrease under osmotic stress, while the rate of generation of superoxide free radicals in leaves increased. MDA content and the activity of SOD, POD [peroxidase] and CAT [catalase] tended to change with the variation in oxygen generation. The process of MDA increase was negatively correlated with water potential and positively with RPMP (relative plasma membrane permeability). GSH (glutathione oxidized form) and AsA (ascorbic acid) content dropped under osmotic stress. The cv. Baipi No.1 was highly resistant to drought, which was manifested in the smaller extent of increase in RPMP, oxygen radical generation and MDA content, and in slower decrease in SOD, POD and CAT activity and AsA content (Chen *et al.*, 2000).

Moderate water stress (-0.075 MPa) induced by PEG-6000, and its interaction with 20 mM calcium chloride studied by Usha *et al.* (1999) in groundnut seedlings aged (24-168 h) reveals that protein content in the embryonic axis of water stressed seedlings became progressively lower but increased in stressed seedlings treated with 40 dS/m CaCl<sub>2</sub>. Addition of CaCl<sub>2</sub> to stressed seedlings increased proline oxidase activity and decreased proline accumulation. Accumulation of putrescine in the embryonic axis was observed in water stressed seedlings, associated with increased arginine decarboxylase activity. Addition of CaCl<sub>2</sub> to the water stressed seedlings decreased putrescine content and arginine decarboxylase activity. Thus Ca alleviates water stress by modulating the levels of proline and putrescine, which are the principal reserves of nitrogenous compounds.

In another study on water stress induced by PEG 6000 and the ameliorative effect of Ca<sup>2+</sup> on changes in calmodulin, Ca<sup>2+</sup>, protein contents and protease [proteinase] activity during seedling growth of two groundnut cvs. TPT 1 and TPT 4, Sulochana and Savithamma, (2002) reported quantitative variations of these in cotyledons and embryonic axis of seedlings and higher protease activity, lower calcium, calmodulin contents were observed in PEG-treated seedlings, however CaCl<sub>2</sub>-treatment maintained higher levels of calcium, calmodulin contents and lower levels of protease activity. A protein with 76 kDa molecular weight was observed in PEG-

treated seedlings, whereas lower molecular weight proteins of 24, 30 and 33 kDa were observed in  $\text{CaCl}_2$ -treated seedlings (Sulochana and Savithamma, 2002). Further studies on these cultivars seedlings treated with PEG, showed an increase in lipid peroxidation, peroxidase activity and decrease in CaM content, superoxide dismutase and catalase activities (Sulochana *et al.*, 2002). The calcium chloride treated seedlings maintained higher levels of CaM content, SOD and CAT activities suggesting amelioration of adverse effects of PEG on membrane deterioration by calcium chloride by modulating the lipid peroxidation and peroxidase activity and maintaining higher levels of CaM and scavenger enzymes such as SOD and CAT and the cv. TPT 4 appears to be more tolerant to water stress than the TPT 1 (Sulochana *et al.*, 2002).

In continuation the moderate water stress (-1 MPa) induced by PEG-6000 and its interaction with 20 mM  $\text{CaCl}_2$  when studied on calmodulin (CaM) and proline contents and activity of proline oxidase in cotyledons and embryonic axis during seedling growth of groundnut cultivars (TPT 1 and TPT 4), the CaM content in cotyledons of water-stressed seedlings decreased progressively after treatment, however,  $\text{CaCl}_2$ -treated seedlings maintained higher levels of CaM and proline oxidase activity and lower levels of proline content (Sulochana and Savithamma, 2001). Calcium appears to ameliorate the water stress by maintaining higher levels of CaM and lower levels of proline by modulating the activity of proline oxidase (Sulochana and Savithamma, 2001). The acid phosphatase (ACPH) activity was low in the seedlings subjected to water stress, but, higher in  $\text{CaCl}_2$ -treated seedlings and  $\text{Ca}^{2+}$  maintained higher levels of ACPH activity in the seedlings of TPT 4 than that of TPT 1 indicating that  $\text{Ca}^{2+}$  modulates the levels of enzyme activity under water stress (Sulochana and Savithamma, 2003).

White grubs larvae damage the root system of groundnut Chitra cv plants. Simulated white grub damage was created by cutting the roots of plants at 10, 20 and 30 cm from the top soil surface at 30 DAS in one set and at 60 DAS in the other set under both normal and drought conditions. The root cut reduced RWC, transpiration and the reduction was highest in plants with roots cut at 10 cm and the lowest in plants with roots cut at 30 cm. Proline content and peroxidase activity increased with the increase in the per cent root cut and the magnitude of increase in proline and peroxidase was almost 2-3 times of the control, in plants whose; roots were cut at 30 or 60 DAS. The roots damaged at 60 DAS reduced the seed yield to a greater extent than the roots damaged at 30 DAS (Yadav *et al.*, 2007). Low soil temperature inhibited nodulation and nitrogen fixation of rhizoma groundnut [*Arachis glabrata*] cv. Florigraze. Water stress limited the development of new nodules and stimulated nodule senescence. N fertilizer application stimulated specific and total nitrogenase activity in spring but inhibited nodule and total nitrogenase activity in summer and autumn. During establishment, Florigraze competed strongly with associated *C. dactylon* for available N fertilizer (Valentim, 1989).

Nodulation and  $\text{N}_2$  ( $\text{C}_2\text{H}_2$ ) fixation were studied in cowpeas and groundnuts during water stress and recovery by withhold water for 5, 6 or 7 d, and leaf water potential and nitrogenase activity measured before and 2, 5, 24, 48, 72 and 120 h after rewatering. In plants relieved from water stress, leaf water-potential recovered much faster than nitrogenase activity in both species, and the recovery ability depended on

the intensity of water stress. Nitrogenase activity recovered much faster in groundnuts than in cowpeas, even from a relatively higher level of stress. This was partly due to the lack of nodule shedding in groundnuts, while severe shedding of nodules in cowpeas did not permit the recovery of activity, particularly at higher stress levels. Leghaemoglobin was more stable in groundnut than in cowpea nodules. Water stress led to accumulation of total soluble sugars in groundnut nodules, while there was no change in cowpeas (Venkateswarlu *et al.*, 1990).

Water status and N metabolism of groundnut cv. M-13 and M-145 were examined during a period of water stress and recovery. 10-day-old seedlings grown in controlled environment were exposed to sol. of PEG (mol. wt. 6000, osmotic potential -5 or -8 bar) for 1 wk when the stress was relieved by replacing the PEG sol. with a nutrient sol. M-13, despite its lower relative turgidity during stress, was better able to preserve its protein conc. and nitrate reductase activity and recover to a normal state within 3 days of the relief of stress, but M-145 failed to recover within this period (Saini and Srivastava, 1981). In a growth chamber, groundnut cv. Yue You 551-116 seedlings at the 3-leaf stage treated with 5 ppm PP 333 (paclobutrazol) or 150 ppm. CCC [chlormequat], when one day later, PEG solution at 10-3 mol/litre was used to create water stress in the rhizosphere, both PP 333 and CCC treatments increased peroxidase activity compared with untreated seedlings, though the zymogram patterns of the 2 treatments were different. More bands were observed in the isozymograms of the treated seedlings than in the control (Li and Pan, 1990).

At low water potentials root elongation still continues, while shoot growth and elongation have completely ceased at similar water potentials. This differential response of root and shoot is an adaptation by plants to avoid excessive dehydration while tapping moisture available at lower depths of the dehydrating soil. The stress regulator abscisic acid (ABA) has been implicated in this unique adaptation of plants to water stress and this has been demonstrated convincingly in maize using ABA-deficient mutants. The ABA accumulating capacity of 2 distinct cultivars of finger millet and groundnut, differing in root elongation under water stress, the root ABA content was not significantly different in water-stressed plants of these cultivars, although differences in root growth and root elongation at low  $\psi_w$  were distinctly different. Tissue sensitivity to ABA and compartmentation under stress could influence these observed differences in root growth in the cultivars rather than the ABA accumulating capacity (Suma *et al.*, 2006).

Groundnut genotypes at normal and water stress conditions for 30 days were studied in the greenhouse in order to investigate the enzymatic behaviour and to determine the best enzyme systems for the production of molecular markers associated with water stress. Normal and stressed leaflets and root tissues were collected at 45 DAS and analysed by via PAGE with a continuous buffer system and studied esterase (EST), peroxidase (POX), malate dehydrogenase (MDH), superoxide dismutase, acid phosphatase (ACP) and leucineaminopeptidase [cytosol aminopeptidase] where POX and ACP in the roots gave the highest contribution to the differentiation process between genotypes and treatments; The EST and MDH contributed towards genotypes differentiation, only under stressed conditions (Santos dos *et al.*, 1998). Under water deficit condition, production of reactive oxygen species in terms of  $H_2O_2$  and

superoxide radical (SOR), and lipid peroxidation was more at both flowering and pod development stages compared to vegetative stage in groundnut. The study concluded cultivars ICGS 44 and TAG 24 showed better tolerance capacity by maintaining higher relative water content and antioxidant enzyme activities, and sustaining much less membrane injury due to imposition of water-deficit stress (Chakraborty *et al.*, 2012).

### 3.10. Molecular Physiology

The eco-physiological responses of groundnut are studied in details, however little is known about the molecular events involved in its adaptive responses to drought. The involvement of membrane phospholipid and protein degrading enzymes as well as protective proteins such as “late embryogenesis-abundant” (LEA) protein in groundnut adaptive responses to drought were studied and Partial cDNAs encoding putative phospholipase Da, cysteine protease, serine protease and a full-length cDNA encoding a LEA protein were cloned and their expression in response to progressive water deficit and rehydration was compared between cultivars differing in their tolerance to drought by Drame *et al.* (2007) and differential gene expression pattern according to either water deficit intensity and cultivar’s tolerance to drought and a good correspondence between the molecular responses of the cultivars and their physiological responses was found. Molecular characters, as detectable at an early stage, could therefore be efficiently integrated in groundnut breeding programmes for drought adaptation.

An incomplete half-diallel cross performed on an original population under recurrent selection for drought adaptation analysed, the study confirmed the weak heritability of yields and the best predictor of pod yield was the pod yield itself. In contrast, the study of the genetic correlations showed that a selection for high haulm yield could lead to poor pod maturity under drought constraint. The selection indices were performed and used to estimate genetic gains relative to the main agronomic characters according to selection pressure. The genetic variability of phenological, agronomic and physiological characters was studied in two series of quasi-isogenic early lines where genetic variability was expressed in these lines despite its closeness. The correlations between yield and fluorescence parameters were significant but not stable across lines and environments showing that groundnuts have different drought adaptation strategies according to genetic background and drought pattern. At the molecular level with three reference cultivars involving both recurrent parents of the precedent study, the gene transcript kinetics under drought, obtained using RT-PCR, showed that phospholipase D and cysteine proteinase gene expressions were stimulated by stress in the most susceptible cultivars, while there was higher LEA gene expression in the resistant one (Clave *et al.*, 2007).

Improvement of drought tolerance is an important area of research for crop breeding programmes. Recent advances in the area of crop genomics offer tools to assist in breeding (Varshney *et al.*, 2005, 2006). The identification of genomic regions associated with drought tolerance would enable breeders to develop improved cultivars with increased drought tolerance using marker-assisted selection (Ribaut *et al.*, 1996). There are RFLP (Restricted Fragment Length Polymorphism) maps of wild

type x cultivar crosses but the polymorphisms are too low for a cultivated x cultivated species cross; therefore, new markers are needed (Burow *et al.*, 2001). A considerable number of SSR sequences have been identified from groundnut genome by several research groups (Hopkins *et al.*, 1999; He *et al.*, 2003; Ferguson *et al.*, 2004; Moretzsohn *et al.*, 2005; Proite *et al.*, 2007; Cuc *et al.*, 2008) which would enable breeders and molecular biologists to use this wide variability for further improvement of drought tolerance in groundnut. Differential display reverse transcriptase PCR was used to identify genes induced and suppressed in groundnut seed during drought. A total of 1235 differential display products were observed in irrigated samples, compared to 950 differential display products in stressed leaf samples (Jain *et al.*, 2001). Many families of transcription factors including AP2/EREBP (AhWSI 279), bHLH (AhWSI 111, AhWSI 40), bZIP (AhWSI 20), CCAAT box (AhWSI 117), Homeobox (AhWSI 6 11) which showed differential expression in groundnut under drought stress.

Twenty two groundnut genotypes evaluated for water stress-regulated proteins by Katam *et al.* (2007) and to determine possible role of these proteins in groundnut acclimatization and adaptation to drought in pots under greenhouse conditions till 120 days and subjected to water stress by withholding irrigation at soil water potential 10, 16, 28 and 38 centibars at 7, 14, 21 and 28-day stress periods, respectively. The study shows that both the drought-tolerant and drought-susceptible genotypes responded similarly during the brief stress for 3 days, but during prolonged stress conditions (>3 days) drought-tolerant genotypes (Vemana, K 1375) are able to maintain expression of certain proteins (molecular weight between 14 kDa and 70 kDa) while in drought-susceptible genotypes (M 13, JL 24), these proteins are suppressed indicating their role in stress tolerance. Evaluation of groundnut genotypes with diverse drought tolerance characteristics for determining differences in their response to drought stress showed varying levels of protein expression, suppression or over-expression of leaf proteins among the genotypes. Polypeptide matches of the selected 2D-resolved proteins were found to be similar with the proteins of ultraviolet-B repressive rubiscoactivase, glyceraldehyde-3-phosphate dehydrogenase, ribulosebisphosphate carboxylase, phosphoribulokinase, cytochrome b6-f complex and oxygen-evolving enhancer protein (Katam *et al.*, 2007).

The NAC transcription factors existed differentially in plant are the new transcription regulatory factors with multiple biological functions. Two NAC-like genes from groundnut were cloned by RT-PCR and RACE methods, named AhNAC2 and AhNAC3 (Gene Bank accession Nos. EU755023 and EU755022), which contained an ORF of 1050 bp and 1008 bp and encoded 349 and 335 amino acids, respectively. Gene sequence analysis showed that the putative protein of both genes contained a conserved NAC domain and highly different C terminal, which were the typical characteristics of NAC transcription factors. The transcription levels of the 2 genes when investigated by semi-quantitative RT-PCR, and the result showed that the expressions of AhNAC2 and AhNAC3 genes were enhanced by ABA, GA<sub>3</sub>, water stress and cold stress, respectively. Furthermore, the 2 genes expressed constitutively in groundnut tissues and their expression patterns were different in various tissues. In conclusion, AhNAC2 and AhNAC3 genes isolated from groundnut were new members of the NAC transcription factor family and their comparison to RD26

(AT4G27410) revealed a high amino acid homology, they play key roles in ABA signal transduction and drought response in groundnut (Liu and Li, 2009).

A study to test whether DREB1A gene driven by stress inducible rd 29A promoter could have an effect on groundnut root growth under water deficit using lysimetric system and changes in the ET response and in the rooting pattern upon exposure to water deficit in 5 transgenic events and their wild type (WT) parent clearly indicated that DREB1A induced a root response under water deficit conditions (Vadez *et al.*, 2007). This response enhanced root growth under water deficit in particular in the deep soil layers. Consequently, water uptake under water deficit was enhanced, up to 20-30 per cent in some transgenics compared to the WT. This water uptake was well related ( $r^2=0.91$ ) with the root dry weight below the 40 cm soil depth. Finally, it appeared that the putative effect of DREB1A on root under water stress conditions was due to an effect on the root/shoot ratio, which was dramatically increased under water stress in all transgenic lines (Vadez *et al.*, 2007).

Transgenic plants carrying genes for abiotic stress tolerance are being developed for water stress management. Structural genes (key enzymes for osmolyte biosynthesis, such as proline, glycine-betaine, mannitol and trehalose, redox proteins and detoxifying enzymes, stress-induced LEA proteins) and regulatory genes, including dehydration-responsive, element-binding (DREB) factors, Zinc finger proteins, and NAC transcription factor genes, are being used. Using *Agrobacterium* [*Rhizobium*] and particle gun methods, transgenics carrying different genes related to drought tolerance have been developed in rice, wheat, maize, sugarcane, tobacco, *Arabidopsis thaliana* and groundnut (Gosal *et al.*, 2009). In general, drought stress-tolerant transgenics are either under pot experiments or under contained field evaluation. Molecular markers are being used to identify drought-related quantitative trait loci and their efficient transfer into commercially grown cultivars (Gosal *et al.*, 2009).

Novel stress responsive genes were identified following subtractive hybridization of cDNA synthesized from RNA isolated from stress and unstressed groundnut leaves. One of the cloned genes (Gdi15) exhibited increased expression in stressed leaves. Sequence analysis indicated that it has significant homology with flavonol 3-O-glucosyltransferase, a gene involved in anthocyanin biosynthesis and shows increased expression of flavonol 3-O-glucosyltransferase under desiccation stress (Gopalakrishna, 2001).

Drought and high temperatures are conducive to *Aspergillus flavus* infection and aflatoxin contamination. The molecular tools, proteomics, DD-RT-PCR (differential display reverse transcription-polymerase chain reaction), expressed sequence tag (EST) and gene chip technology (macro/microarray) to study gene expression in response to drought stress, and genetic transformation, were studied by Guo *et al.* (2003) using DD-RT-PCR to display genes expressed in groundnut and maize grown under drought stress vs. irrigated conditions use EST/microarray technology to study the whole genome as influenced by drought stress in maize and groundnut, and *A. flavus* ESTs to better understand the genetic control and regulation of toxin biosynthesis (Guo *et al.*, 2003).

### 3.11. Leaf Membrane Injury

Two groundnut cultivars grown for 13 weeks under water controlled conditions in pots, the cultivar Falcon (F) showed characteristics of drought tolerance, while cultivar Local (L) showed those of drought susceptibility. Falcon showed an osmotic adjustment mechanism that enables it to withstand short-term drought stress. The membranes of the Falcon were less injured under drought stress and maintained higher RWC (water saturation deficit, WSD) and relatively low relative saturation deficit (RSD) as compared with the cultivar Local. Additionally, proline was substantially more accumulated in this cultivar. Therefore, cultivar Falcon was classified as drought tolerator and cultivar Local as drought avoider. The relative water content (RWC), relative saturation deficit (RSD), cell membrane integrity (CMI) and proline content were effective criteria for detecting drought tolerance strategies taking into account the growth stage and duration of the stress period, while the water retention capacity (WRC) did not show any significant relation with drought tolerance (Quilambo, 2004).

The effect of different physiological indexes on cell injury of detached groundnut leaves under osmotic stress showed significant correlations between water potential, relative plasma membrane permeability (RPMP), MDA, superoxides and superoxide dismutase activity (SOD). The correlations between catalase (CAT), peroxide (POD), glutathione synthase (GSH), ascorbic acid and water potential, RPMP, superoxides, MDA and SOD varied depending on the cultivars. The effects of water potential on the productive elasticities of RPMP, MDA, superoxides and SOD were negative, while the effects of SOD on the productive elasticities of RPMP, MDA and superoxides progressively decreased. Similarly, a progressive decrease was observed in the effect of superoxides on the productive elasticities of RPMP and MDA. The productive elasticities and marginal yields varied with cultivars exhibiting varying drought resistance (Zhu *et al.*, 2001). Groundnut seedlings grown in nutrient solution containing 0-400 mg methyl jasmonate/litre, and transferred at the 3-leaf stage to PEG solution for 3 d, Methyl jasmonate decreased permeability of the plasma membrane, and increased activities of superoxide dismutase and catalase, during drought stress. Methyl jasmonate also induced the formation of new superoxide dismutase isoenzymes, increased ascorbic acid content, and decreased levels of malondialdehyde (Pan *et al.*, 1995).

Cell membrane stability (CMS) in suspension cultures of groundnuts cv. Kadiri 3 and JL 24 studied after incorporation of various doses (0-20 per cent) of PEG in the culture medium showed a negative relationship between PEG concentration and membrane stability measured as electrolyte leakage. The CMS values in the cell cultures correlated well with the whole plant tissue and permitted the differentiation of cultivars based on their known response to drought stress. The cell membrane stability was lower (more electrolyte leakage) in culture as compared with the intact plant tissue. Kadiri 3, the drought tolerant cultivar maintained higher CMS than JL 24, the drought susceptible one. Increasing PEG levels, K concentration in cultured cells declined in both cultivars, however, Kadiri 3 maintained higher K values than JL 24 accompanied with greater cell membrane stability. Total soluble sugars also increased with increasing stress in both cultivars; CMS test can be used under in vitro conditions to



differentiate the drought tolerant and susceptible cultivars, and that the cellular K level has a positive relationship with membrane stability (Venkateswarlu and Ramesh, 1993).

Maintenance of membrane integrity under stress reflects broadly intrinsic tolerance. Leaf discs of 1 cm diameter from 14 day old plants of groundnut subjected to rapid (open Petri dish; dry filter paper) and slow (closed Petri dish) desiccation in a growth chamber at 35°C, 60 per cent RH and 700  $\mu\text{ein}/\text{m}^2\text{s}^{-1}$  light intensity at water loss about 60 per cent, membrane integrity (percentage leakage), was maintained in groundnut in both rapid and slow desiccation stress (Gopalakrishna, 2001). In variety Florman INTA and 6 pure lines under water stress, 9 physiological variables when measured along with yield and its components, and oleic to linoleic acid ratio, the lines fell into groups contrasting in drought tolerance, with the most precise grouping classing Manfredi 420 as tolerant, Florman INTA as susceptible and the rest as intermediate. The correlations between physiological variables and yield traits show that the most tolerant lines were those which could keep their stomata most open during drought stress, without major alterations in membrane stability (Collino *et al.*, 1994).

### 3.12. Diseases

Groundnut wilting caused by *S. rolfsii* [*Corticium rolfsii*] often occurs in wet and hot summer, but severe epidemics have also been observed when wet periods follow protracted dry ones in the groundnut producing regions. March *et al.* (1999) studied the influence of drought stress in predisposing groundnut plants to wilting in cv. Florunner by 8 weeks old subjected to different soil-water regimes and inoculated with sclerotia of *C. rolfsii* in greenhouses. On the inoculation day, leaf water potential ( $\psi_l$ ) of a fully penultimate expanded tetrafoliate leaf when measured using a pressure chamber, leaf PSI of non stressed plants ranged from -0.2 to -0.4 MPa while in wilted plants ranged from -1.2 to -1.4 MPa. Water stress enhances infection by *C. rolfsii* but drench-irrigated plants maintaining soil moisture at water holding capacity did not show infection. Facultative parasites like *C. rolfsii* are usually favoured by conditions that weaken or stress the host (March *et al.*, 1999).

## 4. Impact on Reproductive Growth and Yield Components

There are three major aspects of drought, duration, intensity and timing relative to crop phenophases which vary independently. Water stress delay pod initiation, and the major cause of variability in pod yield and HI is the delay between peg initiation and onset of rapid -pod growth, because once pods were initiated, the proportion of dry matter allocated to reproductive sink was relatively conservative (Stirling and Black 1991). The period of reproductive growth stages in groundnut occurs over a period of nearly two months and moisture stress has a depressing effect on flowering, stem growth and nodulation. No flowering occurs during the stress, but once the stress is removed, there is a flush of flowering depending on the growth stages and sometimes it results in more flowers than control (Singh 2003). The Virginia groundnuts, due to their longer duration, are more tolerant to drought than Spanish and Valencia however the later due to short duration escape the late season drought.

Experiments conducted on Warin soil series at the Agricultural Development Research Center (ADRC), Khon Kaen Province, indicated that adequate water supply should be maintained in order to get optimum yield and yield decreases due to water stress at different growth stages in order of water stress at seed development > at early pod filling > at early growth > at early pegging (Uthai *et al.*, 1993).

Plant population influenced both the temporal and spatial patterns of water use, with high density crops extracting water from lower depths sooner than low density crop. High water use prior to early pod filling in high density crop was associated with more rapid leaf area development (Wright and Bell 1992b). The more rapid water extraction in a high, compared with a low, population density groundnut crop is associated with greater root production at depth (Nageswara Rao *et al.*, 1989). The seed yields with drought for 3 weeks starting week 5 or 6 were 65.5 and 34.1 g/m<sup>2</sup>, resp., compared with 81.9 g without water stress (Zaharah 1986).

#### 4.1. Seed Growth and Pod Development

The early and continuous availability of water until the start of pod filling results in large canopy and during the period of drought stress the transpirational demand increases. The ratio of pod number: peg number reduced from 0.8 in normal irrigated crop to nearly 0.15 in stressed crop (Harris *et al.*, 1988). Moisture stress at flowering reduced phytobiomass and pod yield by limiting the number of mature pods per unit area as compared to stress at pegging and pod formation stages (Rao *et al.*, 1986). Under water stress there is poor pod filling that reduced kernel size, shelling, SMK per cent and lipid content of kernel. Nageswara Rao *et al.* (1989 b) in a study observed that when water deficit occurred during seed filling phase, genotypic yield potential accounted for approximately 90 per cent of the variation in pod yield sensitivity to water deficit, and further elaborated that it is unlikely that breeders will be able to combine high yield potential with low sensitivity to drought spanning the seed filling phase, therefore other important strategies are necessary.

Stirling (1989) in a controlled-environment greenhouse study a finite quantity of water applied to groundnut cv. Kadiri at different stages of the growing season by imposing two levels of soil moisture deficit by withholding or applying limited amounts of irrigation at regular intervals during two periods; sowing to pod initiation and pod initiation to final harvest where shoot DM yields were hardly affected but pod yields were more than 4-fold lower in early- than in late-irrigated stands. The degree-day requirement for peg initiation was similar in all treatments but late irrigation delayed pod development by about 200 degree days. The effect of timing of irrigation on pod yield operated mainly through its influence on the duration of pod production, which was closely linked to the rate and duration of canopy expansion late in the season. The insensitivity of pod yield to early moisture deficits reflected the extreme plasticity of growth and development in groundnuts, since most processes resumed rates similar to the pre-stress levels in early-irrigated stands once stress was released (Stirling 1989).

Bennett *et al.* (1990) in experimental constructed root tube-pegging pan apparatus to allow physical separation of groundnut rooting and pegging zones with independent control of soil water in both zones where satisfactory shoot growth and

pod development of plants occurred. Using the apparatus, the effects of air-dry and moist (7-12 per cent water by wt) pegging zone soil on seed and pod formation when examined, soil water deficits in the pegging zone decreased the number of pods which reached full expansion from 61-48 per cent. Total pod and seed wt, growth rates of pods and seeds and individual pod and seed wt/plant also decreased in air dry treatment. Drought conditions reduced the av. seed wt. of sound mature seed in Florigiant and Florunner but not in Tifspan (Pallas *et al.*, 1977).

Effects of drought on groundnut seed development and quality when studied in Shandong, using cv. Baisha 1016, at soil water-holding capacity controlled at 55-65 per cent, 60-70 per cent and 50-60 per cent at the flowering, fruiting and ripening stages, resp., the most significant effect of drought for 30 days on seeds was at the seed development stage, resulting in 25.1 per cent decrease in 100-seed wt. A drought period of 30 days at the flowering caused a 24.7 per cent decrease of 100-seed wt., while at the the ripening stage it resulted in a 14.6 per cent decrease in 100-seed wt and also reduced seed size and increased the number of shriveled seeds (Yao *et al.*, 1982). The effects of skipping one irrigation during pod initiation, pod development or pod maturity and application of potassium fertilizer (0, 24, 32 and 40 kg K<sub>2</sub>O) on the yield and yield components of groundnut cv. Giza 5 were determined in a field in Egypt where water stress, at pod initiation and pod development, reduced the number and weight of pods and seeds per plant, shelling percentage, pod yield, oil and protein percentages and yield. Potassium application increased the number and weight of pods per plant, number of seeds per plant, 100-seed weight, pod yield, oil and protein percentages, and protein yield compared with the control (Ali 2001).

Golakiya and Patel (1992) imposed 10 combinations of water stress at flowering, peg formation, pod development and pod maturity of J 11 and GG 2 cultivars in lysimeters, and reported that the growth, was curtailed by water stress at any of the growth stages with stress at the flowering stage being the most inhibitive, however yield was reduced most by water stress at pod development due to reduced crop reproductive efficiency. Pod yield was reduced by reductions in fertility index, seed formation coefficient and seed formation efficiency and GG 2 was more drought tolerant than J 11. In Akola, groundnut cv. JL 24 recorded higher pod yield when sown in the last week of June, but sowing extended beyond this period, up to September resulted in progressive reduction in yield even though irrigations were applied when necessary (at 80 mm CPE) to avoid moisture stress across delayed sowings. Number of effective pegs, developed pod number and pod dry weight were influenced by variations in atmospheric temperatures, particularly minimum temperature, and the relative humidity indicating that warmer temperatures and higher relative humidity during crop growth period favourably influenced the yield contributing characters and finally the pod yield (Karunakar *et al.*, 2002).

In Andhra Pradesh the effect of mid-season drought (MSD) and end season drought (ESD) on the yield and yield attributes of 20 groundnut genotypes (11 advanced breeding lines and 9 released varieties) studied by withholding irrigations between 50-100 DAS and 100 DAS to the final harvest, respectively, as against crop receiving full irrigation during the whole crop duration, revealed genotype differences, and genotype environment interaction for pod yield, shelling percentage and HI.

Reduction under both stress conditions was observed for the number of mature pods, pod yield, shelling percentage, 100-kernel weight and HI, indicating that these characters were significantly affected by MSD and ESD, however, percentage sound mature kernel and oil content were reduced only under ESD as it coincided with the seed maturation and oil formation, there was maximum reduction in the number of mature pods (47 per cent) under MSD, followed by pod yield (29.7 per cent) while under ESD for pod yield (41 per cent), followed by the number of mature pods (33 per cent), indicating that number of mature pods was most sensitive to MSD and pod yield to ESD (Suvarna *et al.*, 2002).

In southern Telangana on Alfisols, groundnut generally suffers from mid-season drought reducing crop yields where 18 groundnut genotypes along with a local control (TMV 2), crop experienced a 27 day long dry spell from the beginning of pod initiation to full seed development in 1994, and for 16 days from the beginning of peg initiation to the beginning of pod development in 1995, the pod yields ranged from 0.58 (ICGS 88) to 2.41 t/ha and only K 134 and ICGV 86347 were superior genotype with high yield, but, the yield superiority of these two genotypes was not reflected in their ancillary characters (Thatikunta and Durgaprasad, 1996).

#### 4.2. Partitioning and Harvest Index

The pod yield is a function of transpired water (T), transpiration efficiency (TE) and harvest index (HI), and the TE derived from measurements of carbon isotope discrimination in leaves indicated only small variation (Wright *et al.*, 1991). The variation in HI accounted for the large proportion of variation in yield and recommended to make selection for high HI. The reproductive development is sensitive to drought resulting to poor yield. The strategies to combat drought in genotypes are (i) early production of flowers, pegs and pods, with subsequent filling of the pods at a moderate, but essentially at constant rate despite the drought, (ii) faster development of later developed pegs into pods once water become available after drought late in the season, Drought stress effects on groundnut depend primarily on the stress pattern because genotypic variation is usually of secondary significance. Comparison of various groundnut genotypes indicated that the Acc 847, 55-437 and GNP 1157 tended to have the tallest plants, greatest shoot DM and leaf area and highest pod and seed yields under stress conditions. Seed yields under stressed and non-stressed conditions were 5.40 and 12.17, 4.08 and 10.62 and 4.56 and 18.55 g/plant for Acc 847, 55-437 and GNP 1157, respectively (Rosario and Fajardo, 1988).

In Argentina with two different regimes of water (irrigated (IRR) from sowing to maturity, no water between 47-113 DAS) on groundnut cultivars Florman INTA and Manfredi 393 INTA, the fraction of PAR intercepted, (f), leaf area, pod and vegetative above-ground biomass and leaf carbon dioxide exchange rate (CER) measured periodically during the water deficit period, and leaf area index, degree of leaf folding, canopy extinction coefficient, radiation use efficiency (RUE), partitioning factor, (p), and harvest index (HI) calculated from the measurements. Under water stress, f was reduced in both varieties and the reduction was proportionally higher in Florman INTA as a consequence of a higher leaf area reduction and degree of leaf folding. However, f remained higher in Florman INTA than in Manfredi 393 INTA due to the

enhanced capacity of the former to generate leaf area under non-limiting water supply. RUE values due to their ability to maintain a higher leaf CER were higher in Manfredi 393 INTA than in Florman INTA, both under irrigation as well as under severe water deficit, where they were obtained using a two-parameter exponential model. Partitioning ( $p$ ) to pods under irrigation was greater in Manfredi 393 INTA than in Florman INTA, as a result of a longer pod filling period and higher  $p$ . Towards the end of pod filling, there was a rapid increase of  $p$  in Florman INTA, but too late to improve its HI. Under water stress, the time course of  $p$  for both varieties was lower than in the IRR treatments and consequently, HI at harvest was reduced. Low HI values could be attributed to some extent to the mechanical impedance of the upper soil layer, caused by water deficit. Mechanical impedance alters the relation among  $p$  and HI values obtained under irrigation and water stress. However, even if it is accounted for, cultivars with high HI under IRR conditions usually have high HI under water deficit (Collino *et al.*, 2001).

A two years of study at the ICRISAT Sahelian Centre, near Niamey, Niger, to select groundnut cultivars tolerant of drought and to investigate selection techniques using 36 cultivars known to differ in yield potential grown under rainfed and irrigated conditions. Crop growth rate ( $C$ ) and partitioning coefficient ( $p$ ) were estimated from phenological and final harvest data. The correlation between years was greater for partitioning than for pod yield (implying a higher heritability for  $p$  than yield). Tolerance as determined by a drought susceptibility index for pod yield ( $S_y$ ), crop growth rate ( $S_c$ ) and partitioning ( $S_p$ ) to reproductive sinks showed 13 cultivars to be drought tolerant for either  $C$  or  $p$  or both. The Sahelian cultivars 796, 55-437 and TS 32-1 were the most consistent for drought tolerance. Partitioning was the most important yield component affecting yield differences among cultivars (Ndunguru *et al.*, 1995).

Chapman *et al.* (1993a) in a greenhouse experiment at Queensland, groundnut cultivars grown by withholding water for a period of 3 weeks during 46- 67 DAS, Robut 33, the cultivar with the highest HI, produced greater yield than either Virginia Bunch or McCubbin mainly due to higher number of pods, compared with the other cultivars. When water was withheld from 61-78 DAS, the Virginia type cultivars (Virginia Bunch and Robut-33) produced a greater yield than the Spanish type cultivar (McCubbin). Peg initiation was sensitive even to mild water deficit, but elongation of pegs halted by water deficit could continue after rewatering. This may be an important attribute particularly where intermittent drought occurs. In both water-deficit treatments, peg initiation and elongation in all cultivars halted after about 80 per cent of the extractable soil water had been exhausted. The yield advantage of Robut-33 was mainly in producing a large number of pods prior to water deficit, and in partitioning a greater amount of biomass to pods after rewatering. The Virginia type cultivars were also apparently better able to tolerate the effects of severe water deficit (Chapman *et al.*, 1993a).

In another study Chapman *et al.* (1993b) at Redland Bay in Queensland, groundnut cultivars subjected to a period of reduced water supply during early reproductive development differed in growth responses during and after the period of water deficit and Q 18801, a Virginia type cultivar with a high HI under non water-

limiting conditions, yielded higher than Virginia Bunch and McCubbin (a Spanish type). During the period of water deficit, all cultivars produced similar number of pegs and pods, but greater proportions of these were converted to pods in Q 18801 and McCubbin than in Virginia Bunch. Water deficit delayed the start of the period of rapid pod growth by about 15 d and hence extended the time required to reach maturity. After rewatering, the number of pegs and pods and the leaf area index of Virginia Bunch and McCubbin increased rapidly. In contrast, Q 18801 partitioned more assimilate to pods, achieving a higher average growth rate of individual pods, and consequently a higher total yield of pods and seeds. Thus, selecting cultivars with increased HI (via rapid pod growth at the expense of excess canopy growth) under irrigated conditions may also increase yields following a drought during early reproductive development (Chapman *et al.*, 1993b).

Further study in Queensland, water stress from 84 DAS to maturity, pod and seed yield was reduced by 30 per cent in the Virginia cultivars (Virginia Bunch and Robut 33) and by 45 per cent in a Spanish type cultivar, McCubbin (Chapman *et al.*, 1993d). The Virginia type cultivars also extracted water from a greater depth. Robut 33, a cultivar with a high HI, produced the greatest yield under both well-watered and water-stressed conditions. In all cultivars, potential pod number had been almost achieved prior to the start of the period of water deficit. However, low pod number rather than small pod size, was mainly responsible for the decrease in yield. Part of the yield advantage of Robut 33 lay in initiating a large number of pods prior to the period of water deficit (Chapman *et al.*, 1993d). This greater synchrony of development compared with the other Virginia type cultivar, created a greater sink for assimilate prior to the period of water deficit. During the first 3 weeks period of water deficit, Robut-33 had the highest CGR and was thus able to produce the most pod biomass. Thus characteristics of early and rapid pod growth and high HI were more important in determining yield under water deficit than the amount of water extracted from the soil (Chapman *et al.*, 1993d).

Parameters related to drought tolerance were studied by Chavan *et al.* (1992) in 29 genotypes grown during the rainy seasons under natural conditions or deprived of moisture for 20 days after flowering, where among the spreading group DVR 50 gave the highest yield under both natural and moisture-stress conditions (1268 and 885 kg/ha, respectively), and had a high HI under both conditions and among the bunch group, CGC 4018 gave the highest yield under both conditions (1561 and 1067 kg/ha, respectively). But the best drought index was recorded for LG 42 in the spreading group (14.3) by ICGS 35-1 in the bunch group (18.4). Overall, DVR 50 was the most efficient under both conditions for pod yield, HI and plant-water status (leaf-water potential). Greenberg *et al.* (1992) evaluated 36 groundnut genotypes of varied origin for yield, crop growth rates (C) and partitioning to reproductive sinks (p) in 3 trials at Niamey by altering the irrigation and sowing date so as to vary the amount of water available either throughout the crops' life or through the grain filling phase establishing 5 different environments. Although differences in C existed, differences in the stability of p were the dominant attribute of genotypes adapted to the drought prone Sahelian region but these differences were more attributable to tolerance of temperature and/or humidity than water stress. Canopy temperatures

relative to air (CATD) were strongly correlated with the value of C, but not with yield (Greenberg *et al.*, 1992).

Drought resistance is an important character for increasing groundnut yields in the sub-humid, dry zone of Sri Lanka and to determine the effect of soil water deficit on vegetative growth and seed yield, and the physiological basis of yield of groundnut under using seven groundnut genotypes (Tissa, ANKG 2, Red Spanish, N 45, ICGV86015, ICGV 86143 and ICGV 86149) de Costa *et al.* (2001) studied under well-watered (90 per cent available water) and water-stressed (30 per cent available water) conditions in pots (12 kg) in a glasshouse at Maha Illuppallama, Sri Lanka, where water stress significantly reduced leaf area, final total dry weight and seed yield. Final total dry weight and yield showed significant genotypic variation under both water regimes but did not show significant genotype x water regime interaction. The highest seed yield under water-stressed conditions was by ICGV 86015, but by ICGV 86149 under well-watered conditions. A greater partitioning of dry matter to seeds (*i.e.* greater HI) was required to achieve high groundnut yields under water stress, but dry matter partitioning was not a yield-determining parameter under well-watered conditions where a greater capacity for total biomass production was required to achieve high yields. Under water-stressed conditions, groundnut yields were positively correlated with pod number per plant, seed weight and the number of primary roots per plant (de Costa *et al.*, 2001).

#### 4.3. Yield and Yield Attributes

The yield is a function of many plant and environmental factors and moisture stress play an important role particularly the stage at which moisture stress occurs. The yield losses (per cent) due to mid season drought are estimated as: Yield loss (per cent) =  $100(1 - D_y/W_y)$ , where,  $W_y$  is the pod yield under adequate irrigation and  $D_y$  is the pod yield under drought treatment. The yield reductions have been reported to be 22, 18, 47 and 47 per cent, respectively when drought was imposed from 10-30, 30-50, 50-80 and 80-120 DAS respectively (Billaz and Ochos 1961). The greatest yield reduction in 50-80 days stress treatment corresponds to, peak flowering to early pod filling stage. Meisner and Karnok (1992) observed the pod yield reduction of 49 and 37 per cent by water stresses imposed at 50-80 and 80-120 DAP and suggested that adequate moisture during this period is critical for obtaining maximum yield. The pod yield potential accounted for less of the variation in drought sensitivity (15-64 per cent) in the early and mid-season droughts (Nageswara Rao *et al.*, 1989b). For these circumstances it may be possible to identify genotypes with both high yield potential and relatively low drought sensitivity. Correlation and path coefficients were worked out for nine traits involving 40 hybrids and 14 parents in groundnut where pod yield exhibited significant positive association with pods per plant, dry matter production, kernel weight and harvest index. Path analysis revealed maximum direct effect of pods per plant followed by dry matter production, and kernel weight on pod yield (Vaithiyalingan, 2010).

Ravindra *et al.* (1990) observed that moisture stress at flowering (45-70 DAS) and pod development (60-90 DAS) phases was highly detrimental to leaf area development, dry matter production, pod formation and yield in comparison with stress at the

vegetative phase (20-50 DAS) and the reduction in yield was 57 and 66 per cent, respectively due to moisture stress at these stages. The recovery of growth from water stress was better after relief at the vegetative phase than at later growth phases. Nautiyal *et al.* (1999a) reported that transient soil-moisture-deficit stress for 25 days, at the vegetative phase (20-45 DAS) followed by two relief irrigations at an interval of 5 days, resulted in closely synchronized flowering, greater conversion of flowers to pods and higher pod yield and total biomass accumulation indicating that stress in the vegetative phase was beneficial for groundnut growth and pod yields, but was highly detrimental when imposed at flowering (40-65 DAS) and pod development (60-85 DAS). Nageswara Rao *et al.* (1985) while studying with Robut 33-1 (a 140-150 days crop) observed maximum reduction in kernel yield when stress was imposed during seed filling phase *i.e.* 93 DAS onwards however the treatment receiving 12-15 per cent less water than control during the early phase (line source irrigation at 11 and 21 days followed by no irrigation up to 50 DAS) increased the pod yield by 13-19 per cent over fully irrigated (irrigation at 50 per cent FC) treatment (Nageswara Rao *et al.*, 1988). The increase in yield due to pre-flowering drought is mainly due to promotion of root growth during water stress which promoted subsequent growth during pod fills and inhibition of number of vegetative sites (leaves and branches).

On a medium black calcareous soils at Junagadh water stress at flowering, pegging, pod formation and pod development stages of groundnut cv. GG 2 gave pod yields of 1.43, 1.18, 1.07 and 1.00 t/ha compared with 2.25 t/ha with normal irrigation (Sakarvadia and Yadav 1994). The groundnut cv. GAUG 1 grown in field at -0.3 bar (normal), -0.6 bar and -0.9 bar (corresponding to irrigations at intervals of 7-11, 13-16 and 17-21 days, respectively) water stress adversely affected all the growth, yield and quality parameters like oil and protein content, however potassium application (40 kg K<sub>2</sub>O ha<sup>-1</sup>) decreased these negative effects of water stress on yield and quality (Umar *et al.*, 1997). Water stress for 25-30 days during the vegetative, flowering or pod development stages in Spanish-type groundnuts cv. J 11 and GG 2 reduced pod yield. Water stress during the vegetative stage had less of an effect on pod yield, the number of mature pods/plant, number of nodules/plant, plant DM and N uptake than water stress at later developmental stages (Kulkarni *et al.*, 1988).

The moisture stress imposed by withholding irrigation at early vegetative, flowering, peg penetration, pod initiation, or pod development stage in groundnut cv. AK 12-24 in Bhubaneswar, India, during the rabi the highest number of pods and 100-kernel weight were recorded for non-stressed plants and highest shelling percentage obtained with irrigation based on stress day index (six irrigations) and with the control. Plants stressed at the peg penetration stage produced the lowest number of pods per plant and 100-kernel weight, while those stressed at the flowering stage had the lowest shelling percentage, and lowest yield. Stress at the early vegetative stage, which had the least effect on yield and yield attributes, shortened the flowering period and induced effective pod-filling (Kar *et al.*, 2002).

Groundnut cv. TMV 2 exposed to moisture stress at different growth stages by sowing on different dates indicated that moisture stress during the vegetative, flowering, pegging, pod setting and early pod development stages markedly reduced pod yield, but a high pod yield of 2.62 t/ha was obtained even though the crop was



exposed to moisture stress during the pod development and maturation stages (Raju *et al.*, 1981). The groundnut cv. SB XI irrigated at irrigation water IW: CPE ratios of 0.75 or 0.5 for groundnuts (40 mm/irrigation) during the periods 0-40, 40-80, 80-120 d after sowing, irrigation at IW: CPE ratio of 0.5 in all 3 periods gave 24 per cent less yields than with irrigation at IW: CPE ratio 0.75 throughout in groundnuts. Water stress (IW: CPE 0.5) only during the early or late period of growth did not reduce yields substantially, on the other hand water stress 40-80 d after sowing was most harmful (Patil and Gangavane, 1990). In an lysimeter experiment during summer at Junagadh water stress at flowering (28-48 d after emergence), pegging (40-60 d), pod development (55-75 d) and pod maturation (75-95 d) stages reduced pod yield by 27, 45, 56 and 6.0 per cent, respectively in J 11 and 13, 15, 38 and 6 per cent respectively in GAUG 10 (Golakiya, 1993).

The moisture stress effect using water requirement satisfaction index (WRSI) was studied on the pod yield of groundnut cultivars ICGS 44 and TMV 2 at Hyderabad, India during kharif season where a proportional reduction in pod yield with decreasing WRSI was observed and a yield prediction model derived from the WRSI and pod yield was prepared (Reddy *et al.*, 2003). In Hyderabad, on Alfisol, during rabi season groundnut grown under control ( $T_1$ ) and moisture stress between 40-75 DAS ( $T_2$ ); 30-75 DAS ( $T_3$ ); 85-105 DAS ( $T_4$ ); 105-135 DAS ( $T_5$ ); 20-40 DAS ( $T_6$ ) reveals that moisture stress at different phenophases showed no significant difference in final biomass production at 120 DAS, but affected the assimilate partition to pod (Kumar and Reddy 2003). Under stress-free environment during crop growth period, last 25-30 days growth period, prior to maturity no dry matter accumulation took place either by giving three irrigations ( $T_1$ ) or without any irrigation ( $T_5$ ). Even prolonged moisture stress of 45 days coinciding pre-flowering to seed initiation (30-75 DAS) did not affect the ultimate dry matter production. The pod yield was highest in  $T_6$  (2002 kg ha<sup>-1</sup>) which was on par with  $T_1$  (1971 kg ha<sup>-1</sup>), while  $T_5$  resulted to a significantly lower pod yield (1770 kg ha<sup>-1</sup>). Irrigations at sowing, 10, 40, 60, 70, 80, 90, 105 and 115 DAS instead of 14 irrigations at 10 days interval during rabi season had similar effect on pod yield (Kumar and Reddy 2003).

Nigam *et al.* (2005) in a field trial consisting of 192 genotypes (96 each Tr and E selections, using genetic material from three common crosses and one institute-specific cross from four collaborating institutes in India total seven crosses each contributing six genotypes) grown in a 4x48 alpha design in 12 season x location environments in India, the selection efficiency of Tr relative to E, RETr, was estimated using the genetic concept of response to selection. Based on all the 12 environments, the two selection methods performed more or less similarly (RETr=1.045). When the 12 environments were grouped into rainy and post-rainy season, the relative response to selection in Tr method was higher in the rainy than in the post-rainy season (RETr=1.220 vs 0.657) due to a higher genetic variance, lower G x E, and high h<sup>2</sup>. When the 12 environments were classified into four clusters based on plant extractable soil-water availability, the selection method Tr was superior to E in three of the four clusters (RETr=1.495, 0.612, 1.308, and 1.144) due to an increase in genetic variance and h<sup>2</sup> under Tr in clustered environments. Although the crosses exhibited significant differences for kernel yield, the two methods of selection did not interact significantly

with crosses. Both methods contributed more or less equally to the 10 highest-yielding selections (six for E and four for Tr). The six E selections had a higher kernel yield, higher transpiration (T), and nearly equal transpiration efficiency (TE) and Harvest Index (HI) relative to four Tr selections. The yield advantage in E selections came largely from greater T, which would likely not be an advantage in water-deficient environments. From the results of these multi-environment studies, it is evident that Tr method did not show a consistent superiority over E method of drought resistance breeding in producing a higher kernel yield in groundnut. Nonetheless, the integration of physiological traits (or their surrogates) in the selection scheme would be advantageous in selecting genotypes which are more efficient water utilisers or partitioners of photosynthates into economic yield. New biotechnological tools are being explored to increase efficiency of physiological trait-based drought resistance breeding in groundnut (Nigam *et al.*, 2005).

Forty six Spanish and Virginia groundnut genotypes were evaluated for stability for pod yield and 4 associated traits over 3 microenvironments where, 100-seed weight was stable across environments, but no genotype was superior over all 3 environments. Genotypes 559, 563 and 551 performed better under irrigated conditions, while genotypes 564, 565 and 571 tolerated moisture stress and 4081-4 and 4069-1B were stable under both irrigation and moisture stress (Reddy and Gupta 1994).

In a trial during Feb-June, 1988 (hot weather conditions) at Niamey, Niger, 9 groundnut lines were irrigated with 20 or 40 mm water/irrigation every 1, 2 or 3 weeks. Crops gave no pod yield with irrigation every 3 weeks. Genotypes ICGV 87123 and 55-437 gave the highest yields over all irrigation treatments, but gave very low haulm yields. There were large differences in soil moisture contents (0-210 cm layer) between irrigation treatments but not between genotypes. There were considerable differences between genotypes for the difference between crop canopy temp and air temp. This value is related to leaf water potential. A strong negative correlation was found between mid season crop canopy - air temp. difference and pod yield under intermediate water stress conditions (20 mm water/irrigation each week), whereas no correlation was found under low water stress conditions (40 mm water/irrigation each week) or high water stress conditions (20 mm water/irrigation every 2 weeks) (Greenberg and Ndunguru, 1989).

In summer on clay soil at Junagadh the transient soil moisture stress at various growth stages significantly reduced the pod per plants, shelling, 100-kernal weight, HI and oil content and yield of six groundnut genotypes. While, moisture stress at flowering and pod development stages did not affect the productivity of the crop and save about 33 per cent of irrigation water, stress at flowering stage (25-47 DAS) and pod development stage (50-72 DAS) gave 18.5 per cent and 30.6 per cent reduction in pod yield over control, respectively (Vaghasia *et al.*, 2010). In another study at Junagadh, groundnut cvs. J 11 and GG 2 grown in field lysimeters, the greatest yield reduction occurred when water stress was imposed during the pod development stage and GG 2 was more tolerant to drought than J 11 (Patel and Golakiya, 1991). Reduction in pod yields of 4 groundnut cvs. by soil moisture stress of -14 bar during pegging or pod development period was greater than stress during the vegetative

growth or flowering period and the stress decreased N, P and K uptake, which varied with cv (Polara *et al.*, 1984).

Correlation and path coefficients were worked out for nine traits involving 40 hybrids and 14 parents in groundnut. Pod yield exhibited significant positive association with pods per plant, dry matter production, kernel weight and harvest index. Path analysis revealed maximum direct effect of pods per plant followed by dry matter production, and kernel weight on pod yield (Vaithiyalingan *et al.*, 2010).

#### 4.4 Seed Quality

Drought stress affects seed quality adversely. Drought-stressed plants lose moisture from seed or pod which lead to the reduction in the seeds physiological activity, thereby increasing the susceptibility to fungal pathogens. Besides affecting food quality, drought stress is also known to alter nutritional quality of seed proteins in groundnut (Diwedi *et al.*, 1992). The pod yield and quality of groundnut are reduced when less than 30 cm water was received by the crop. Water deficit during seed production affects  $C_2H_2$  and  $CO_2$  production during subsequent germination (Ketring 1991). The most consistent response of water deficit was reduction in the fraction of rapidly growing seedlings (those with hypocotyl-radical longer than 20 mm at 72 h of germination). Water stress at pod initiation and development phase reduced germinability, vigour, seed membrane integrity, embryo RNA content, and chlorophyll synthesis and dehydrogenase activity in cotyledons during germination, however, moisture stress at early vegetative phase increased 100 kernel wt., embryo wt. and seedling vigour index (Nautiyal *et al.*, 1991). Thus water deficit during seed development affects subsequent growth of seedlings and could pose a problem in establishment for the succeeding crop. Thus a minimum of 500 mm of water was necessary to produce a crop of seeds with high potential for germination and high proportion of vigorous seedlings (Ketring 1991).

At ICRISAT, the seeds of groundnut cv. Robut 33-1 grown under moisture stress (emergence to maturity, emergence to peg initiation, first flush of flowering to last pod set and beginning of seed filling to maturity), seeds from plants with moisture stress from emergence to initiation of pegs gave higher field emergence, better seedling vigour and resulted in increased pod and seed yields over the other treatments. Use of seeds from crops grown with moisture stress from flowering to end of pod set resulted in yield reduction (Sarma and Sivakumar, 1987). The seeds from drought treated plants gave lower germination, though their germination energy was higher than that of the control. Drought treatment at the seed development stage reduced seed oil content, but at the flowering and ripening stages showed no significant effect on oil content. Drought at the flowering reduced protein content of seeds, while at seed development and ripening stages it gave seeds with higher protein content than control (Yao *et al.*, 1982).

The cotyledons and embryonic axis of groundnut seeds germinating under moisture stress created by PEG-6000, total soluble proteins and lipids decreased with the advancement of germination but the decline was less under moisture stress conditions. Total free amino acids, proline and non-reducing sugars increased both in cotyledons and embryonic axes with the advancement of germination stage but

decreased with the increase in moisture stress level, the reducing sugar content, however, was higher under moisture stress, indicating that proline cannot be used as an indicator of stress (Sharma *et al.*, 1989). Eight groundnut cultivars grown at Tifton, Georgia by withholding water at 20-50, 50-80, 80-110 or 110-140 d after planting where drought stress early or late in the growing season had little or no effect on seed oil, protein and mineral contents, but stress during mid-season growth affected all components however, only the decreases in oil and copper contents were consistent for all cultivars (Conkerton *et al.*, 1989).

In Spanish groundnut cv. Ak 12-24, J 11, GAUG 1 and GG 3 subjected to soil moisture stress at different crop growth stages, moisture stress during the early vegetative phase resulted in an increase of 100-seed weight and seedling vigour index but stress at the pod initiation/development stage reduced germinability, vigour, seed membrane integrity and embryo RNA content. Moisture stress reduced chlorophyll synthesis and dehydrogenase activity in cotyledons during germination. Growth potential was linearly related to chlorophyll content and dehydrogenase activity during seed germination. Stress during pod development was most detrimental to all physiological and biochemical processes studied (Nautiyal *et al.*, 1991). Experiment conducted at Bijapur to study the effect of water stress (-1, -3, -5, -7, -10 and -12 bar prepared using PEG 6000) in four groundnut genotypes *viz.*, ICG-1930, KRG 228, ICGS 11 and S 206 where seed germination, seedling growth and vigour index decreased significantly with increasing intensity of stress irrespective of cultivars tested, with ICGS 11 and ICG 1930 showing higher seed quality parameters indicating drought tolerance (Pawar, 2011).

Misra and Nautiyal (2005) studied kernel quality components (total sugars, phenolics, protein and fatty acid composition) as influenced by the soil moisture-deficit stress imposed during different phenophases, in the summer season in four Spanish cultivars of groundnut, AK 12-24, J 11, GAUG 1 and GG 2 and observed increase in stearic acid due to stress during pod development in all cultivars except GG 2, increase in palmitic acid only in GAUG 1 and oleic acid in AK 12-24. Compared to the control, soil moisture-deficit stress significantly increased the protein content. There was, however, a greater increase in protein content due to stress during flowering and pod development compared to the stress during vegetative phases. Stress during vegetative (short), and flowering phases significantly reduced the sugar content. The interaction between cultivars and treatments were significant only for the changes in fatty acid composition, protein and sugar contents, but was not significant for phenolic compounds. It is concluded that the changes in the composition of fatty acids and contents of sugars and phenolic compounds are governed more by cultivar and its interaction with the environmental conditions rather than by the time or the intensity of imposed soil moisture-deficit stress.

In groundnut total oil content was not affected by early-season drought (Conkerton *et al.*, 1989; Bhalani and Parameswaran 1992), but declined (up to 3 per cent) under mid-season (50-80 days after sowing (DAS) drought (Conkerton *et al.*, 1989). For late-season drought (110-140 DAS), various studies reported no effect (Conkerton *et al.*, 1989; Musingo *et al.*, 1989) but a decline in total oil content by Bhalani and Parameswaran (1992). No consistent effect on protein content has been

documented due to drought stress at any particular growth period; nor was protein content in any specific genotype always reduced or increased by drought stress (Conkerton *et al.* 1989). However, Musingo *et al.* (1989) reported that late-season (50 days before harvest) drought caused little change in total protein content of groundnut. The effects of drought on oil, protein and fatty acid contents in 12 genotypes differing in seed quality traits by exposing mid-season (40 and 80 DAS) and the end-of-season (80 DAS until harvest) drought at ICRISAT during post-rainy (November-April) seasons reveal that mid-season drought had no effect on the content of oil, protein and fatty acids other than eicosenoic fatty acid. However, end-of-season drought reduced total oil, and linoleic and behenic fatty acid content, and increased total protein and stearic and oleic fatty acid, genotypic interactions. In ICGVs 88369, 88371, 88381, 88382 and 88403, total oil content remained unaffected while oleic fatty acid content increased under end-of-season drought. These were identified as desirable parents for a breeding program to develop cultivars suitable for rainfed cultivation (Dwivedi *et al.*, 1996).

Fatty acid contents in a genotype are affected by drought stress and seed grade. Composition of fatty acid in crop is affected by drought stress. Regardless of intensity, duration and timing of drought, most of the fatty acid and O/L ratio decreased significantly (Hashim *et al.*, 1993). However, some study reported no major changes in the fatty acid composition, except for oleic acid, due to water deficit stress in summer groundnut (Bhalani and Parameswaran 1992). In field trials at Georgia Florunner groundnut (a) irrigated throughout the growing season (140 days) at 0.2 bar matric potential (total 70 cm water) or (b) irrigated at 0.2 bar potential for 30 days and at 15 bar for 40 days with no further irrigation (total 30 cm water), showed leaf water potential -26 and -12 bar in (b) and (a), and seed yield 6.99 and 5.99 t/ha in (a) and (b), respectively, and musty flavour was detected in (b) but not (a) (Pallas, 1983). In another study at Tifton, Georgia, withholding irrigation in groundnut cv. Florunner at the preflowering (20 DAS), pod formation (50 DAS) or maturation (80 DAS) stages altered the fatty acid composition, oleic:linoleic (O:L) ratio, computed iodine value, alpha-tocopherol and gamma-tocopherol contents and grade of groundnut seed. As groundnuts increased in size, regardless of the stage when stressed, long chain saturated fatty acids, eicosenoic acid [gadoleic acid], O:L ratio and alpha-tocopherol decreased significantly. Groundnuts stressed at maturity showed the greatest decrease in the O:L ratio and the greatest increase in the iodine value (Hashim *et al.*, 1993).

Under drought stress complex carbohydrates and proteins are broken down by enzymes into simpler sugars and amino acid residues, respectively and accumulation of compatible solutes in the cell increases the osmotic potential and reduces water loss from the cell. The raffinose family oligosaccharides (RFOs), such as raffinose, stachyose, and verbascose are soluble galactosyl-sucrose carbohydrates. It was also reported that the expression of enzymes related to the biosynthesis of galactinol and RFOs and their intracellular accumulation in plant cells are closely associated with the responses to environmental stresses (Peters *et al.*, 2007).

Water stress at the pod filling stage reduced kernel yield and nitrogen partitioning to reproductive parts. Water stress at all growth stages reduced nitrogen fixation (Venkateswarlu *et al.*, 1991). Huang and Ketring (1985) in a study grew five groundnut

cvs. under rainfed and irrigated conditions during first year and 6 cvs. during 2<sup>nd</sup> year, where Virginia type cvs. had higher ground cover than Spanish types and water relation components differed between rainfed and irrigated treatments at 67 and 81 DAS, but not at 54 DAS and not among cultivars. However, pod yield and percentage sound mature kernels were significantly reduced under rainfed conditions, but no significant differences were observed among cultivars. Yield reductions due to water stress under rainfed conditions were 83-97 per cent.

The 70 day early season drought caused the greatest reduction in SMK, late season 35-day and midseason 70 day droughts reduced subsequent germination by 5 and 9 per cent, respectively, and plant water stress when relieved and leaf diffusion resistances returned to normal (Pallas *et al.*, 1979). According to Sanders *et al.* (1986) agrometeorological studies must include an awareness of the relationship between environment, maturity, and postharvest quality. The post harvest quality of groundnut is the resultant of the particular set of environmental and cultural practices during pod growth and maturation. Seed composition changes dramatically as the crop matures but has relation with environment. A biochemical basis exists for inferior quality in immature groundnut. Drought stress and soil temperature influence maturation rate and thus had an indirect effect on post harvest quality. In a recent study at Junagadh, prolonged water deficit reduces oil and protein content in groundnut kernels leading to loss of nutritional quality. Accumulation of metabolite like glucose, sucrose and raffinose like oligosaccharides plays important role in drought stress tolerance of groundnut. Differential response between different habit groups showed the runner group are more tolerant to water deficit stress compared to bunch type cultivars (Chakraborty *et al.*, 2013).

#### 4.5. Pod and Seed Size

A minimum of 500 mm of water is necessary to produce a crop of seeds with high potential for germination and high proportion of vigorous seedlings, however the large seed size groundnut require more nutrient and hence more water about 700 mm (Singh *et al.*, 2011, 2013). In general the pod yield and quality of groundnut are reduced when less than 300 mm water was received by the crop. Water stress at pod initiation and development phase reduced germinability, vigour, seed membrane integrity and could pose a problem in establishment for the succeeding crop. The pod size tended to be reduced under drought condition (Blakenship *et al.*, 1983). Large seeds of groundnut have greater consumer preference and fetch higher prices in domestic and international markets. In general cultivars belonging to var. *hypogaea* have larger and heavier seeds and those belonging to var. *fastigiata* have smaller seeds. The size of kernel is one of the important factors for export and normally varieties with hundred seed mass of 60 g or more are considered as large seeded groundnut and are preferred for confectionery purpose.

There is very little work reported on the effect of moisture stress on seed size. Drought at flowering reduced the seed size and increased the number of shrivelled kernels (Yao *et al.*, 1983). A drought period of 30 days at the flowering caused a 24.7 per cent decrease of 100-seed wt, while at the ripening stage it resulted in a 14.6 per cent decrease in 100-seed wt and also reduced seed size and increased the number of

shriveled seeds (Yao *et al.*, 1982). Seed size of all cultivars decreased when available water was reduced. Under water stress, Tainan 9 and ICGV 98324 had the biggest seed and seed size of Tainan 9 and ICGV 98324 were reduced by 35 per cent and 29 per cent. Regarding seed size, Khon Kaen 60-3 was the most sensitive cultivar under water stress. Seed size of Khon Kaen 60-3 was reduced by 72 per cent at 1/2 AW.

The National Research Center for Groundnut (now DGR), Junagadh, India, has undertaken programme to develop large seed cultivars more suitable for direct consumption and processing and two seasons of studies on a few promising lines (ICGV33101, PBS 29058 and PBS 29030) possessing large seeded and/or confectionery properties indicated water as the main production factor (Hariprasanna *et al.*, 2004). Kale *et al.* (2000) evaluated eight early bold seeded selections over 4 seasons under irrigated and high management condition and found superior yield in selections TGLPS 2, TGLPS 3, TGLPS 4, TGLPS 6, TGLPS 7 and TGLPS 8 over the large kernel checks *viz.*, TKG 19A and BAU 13, with 71.4 to 80.3 g 100 kernel weight and about 49 to 65 per cent kernels having 100- kernel weight >80 g. Manivel *et al.* (2000) evaluated twelve advanced breeding lines along with controls (B95, Somnath and ICGV 89211) where the 100-seed mass of the test genotypes and controls ranged from 53.9 g (PBS29036) to 76.7g (ICGV 89211) and none of the genotypes were superior over the best control (ICGV 89211). Rajgopal *et al.* (2000) evaluated 118 groundnut accessions for two years. The 100 seed mass ranged from 46.8 g for GG11 to 69.9 g for NRCGs 8939, 5850, 7276, 5505, 750 gave significantly higher 100 seed mass than M 13. These all are mainly due to water constraint during pod filling phases as groundnut at Junagadh most of the year face mid season or terminal drought and one or two protective irrigation are required for getting proper pod filling (Singh *et al.*, 2011, 2013). Planted seed size affects the rate of emergence and seedling vigour significantly and positively associated with increased seed size (Gorbet, 1977).

In Tifton, Georgia, withholding irrigation in groundnuts cv Florunner at the pre-flowering (20 days after sowing, DAS), pod formation (50 DAS) or maturation (80 DAS) stages significantly affect fatty acid composition, oleic:linoleic (O:L) ratio and grade of groundnut seed.

In a study on several groundnut varieties Vorasoot *et al.* (2003) found that under reduced available water, the seed size of all varieties decreased. Under adequate moisture, the variety WEST-20 had the biggest seed size while TG-26 had lowest seed size, but under water stress TAG-24 had biggest seed size. The TG-26 was the more sensitive variety under water stress the seed size of which was reduced by 62 per cent whereas TAG-24 reduces by 41 per cent over control as compare to other varieties. Dry pod size of all varieties decreased under water deficit condition. There was significant interaction between soil water regimes and 100 dry pod weight and TG-26 showed maximum reduction in weight (66 per cent) while TAG-24 showed minimum reduction in weight (38 per cent) over control at higher water stress level (Vorasoot *et al.*, 2003).

In a field trial at Redland Bay, Queensland, from 84 d after sowing to maturity, pod and seed yield was reduced by 30 per cent in the Virginia type of cultivars (Virginia Bunch and Robut-33) and by 45 per cent in a Spanish type cultivar,

McCubbin. Robut-33, a cultivar with a high harvest index (HI), produced the greatest yield under both well-watered and water-stressed conditions. In all cultivars, potential pod number had been almost achieved prior to the start of the period of water deficit. However, low pod number rather than small pod size, was mainly responsible for the decrease in yield (Chapman *et al.*, 1993).

#### 4.6. Aflatoxins and Pest Damages

Drought stress during late stages of pod maturation in groundnut crop during the post rainy season, increased the amount of seed infection by *A. flavus*. A significant, positive, linear relationship was found between water deficit (drought intensity) and seed infection in groundnut genotypes. Genotypic differences for seed infection by *A. flavus* were evident at all levels of drought-stress, but, under the more severe stress conditions, the genotypes resistant to *A. flavus* also had seed infection but low levels (Mehan *et al.*, 1988). *Aspergillus flavus* invasion and aflatoxin contamination in groundnuts are related to drought stress, soil temperature and maturity and small, immature seeds are more likely to be contaminated with *A. flavus* than larger, mature seeds (Sanders *et al.*, 1986). The biochemical composition, fungal contamination, as the tendency toward higher moisture content complicate storage of immature seed and each of these factors predisposes immature seed to rapid quality deterioration in storage (Sanders *et al.*, 1986).

A greenhouse study on seven groundnut genotypes and microplot for two consecutive years to determine peg colonization by *A. flavus* and the effect of drought stress on the susceptibility of shells and kernels to *Aspergillus* colonization and aflatoxin contamination reveals that in general, low soil moisture tension enhanced colonization of shells and kernels and shells of most genotypes were highly colonized after harvest from each moisture regime (Azaizeh *et al.*, 1989). Kernels of all genotypes were more susceptible to *A. flavus* and *A. parasiticus* colonization under both long and short drought stress conditions compared with non-stressed and kernels of TX811956 and TX798736 (short stress treatments) contained lower *Aspergillus* infestation and kernels of genotypes PI 337409 and TX 811956 and TX 798736 contained less aflatoxin (Azaizeh *et al.*, 1989). Fifty groundnut genotypes screened for low aflatoxin contamination under field conditions with two main treatments *i.e.*, irrigated and simulated drought conditions reveals that ICGV 86590, 89104, 94350, 99029, IC 48 and ICGS76 had low aflatoxin levels (<5 ppb) in both the conditions, but no consistent relationship was observed between seed colonization and aflatoxin production (Sudhakar *et al.*, 2007). Also aflatoxin production in groundnut was negatively related with RWC, pod wall integrity and pod wall moisture content at harvest (Sudhakar *et al.*, 2007).

In Georgia, Kisyombe *et al.* (1985) studied 14 groundnut genotypes grown in rain-shaded field microplots under simulated water stress conditions and in plots under normal rainfall conditions, where J 11 and Lampang proved resistant to aflatoxin under both dry and moist field conditions. Although percentage infection of kernels varied with genotype, ranking of genotypes reported to have drought resistance was consistent under both conditions. When 34 genotypes including those tested in microplots were also evaluated for dry seed resistance in the laboratory, J 11



and PI 337409 were highly resistant. Except for J 11 there was no correlation between genotype rankings for resistance to dry seed infection and resistance under field conditions (Kisyombe *et al.*, 1985).

Three groundnut genotypes (ICG 221, 1104 and 1326) drought stressed during the last 58 d before harvest with 8 levels of stress ranging from 1.1 to 25.9 cm of water and the kernels harvested from these were hydrated to 20 per cent moisture and challenged with *A. flavus*, and Fungal colonization, aflatoxin content and phytoalexin accumulation measured the fungal colonization of non-drought-stressed kernels virtually ceased by 3 d after inoculation, when the phytoalexin concentration exceeded 50 µg/g (fresh wt.) of kernels, but in drought-stressed material fungal colonization was inversely related to water supply ( $r$  -0.848 to -0.904, according to genotype), as was aflatoxin production ( $r$  -0.876 to -0.912); the phytoalexin concentration was correlated with water supply when this exceeded 11 cm ( $r$  = 0.696-0.917) (Wotton and Strange 1987).

Early-season moisture stress intensifies groundnut yield and quality losses associated with combined injury from thrips and post emergence herbicides (Funderburk *et al.*, 1998). Whitegrubs (*Scarabaeid* larvae) are major pests of groundnuts in many parts of the tropics and subtropics, attacking both roots and pods and protocols for simulating white grub damage to groundnut roots were developed to predict how feeding by these pests affects plant growth. Pod yield and total biomass were reduced by root-cutting particularly at 51 DAE. Simulated drought reduced pod yield and total biomass, but reductions due to root cutting, were greatest for non-drought treatments. At both 30 and 51 DAE, pod yield reductions were greatest where roots were cut at only 10 cm below the soil surface, and root cut at 30 DAE was totally compensated for by the development of new roots. But cut at 51 DAE initiated very little root regrowth. Both total biomass and pod yield were strongly correlated with plant water use ( $R^2 > 0.9$ ). The protocols developed measure the plant responses to simulated scarab damage and could easily be adapted to measure plant responses to actual scarab damage (Brier *et al.*, 1997).

## 5. Conclusions and Future Research Strategies

Drought is the major abiotic constraint affecting groundnut productivity and quality worldwide. There are three major aspects of drought, duration, intensity and timing which vary with crop phenophases. The groundnut is relatively drought tolerant and an important crop of the semi-arid regions. The plant water-status is the result of a balance between water uptake and loss which has been less understood in groundnut. Though different growth stages have different sensitivity to water deficit, none of these can proceed normally below some minimum water. Groundnut plant contains about 80 per cent of water on fresh weight basis and reduction of the plant water status much below this level causes wilting and affects the rate of several plant functions. The water flow in intact plant under high soil moisture condition is for growth and transpiration and two concepts are expressed about the driving force for transpiration water flow, the water potential differences between the root and leaf as the primary force and hydrostatic and osmotic pressure differences, as the factors determining water flow. The ability of groundnut genotypes to maintain water supply

to leaves using apparent sap velocity ( $V_a$ ) was 0.8-1.1 cm min<sup>-1</sup> and declined with stress in field. Increasing moisture stress from 0 to 6 atm decrease the leaf RWC, increased water saturation deficit and relative saturation deficit, decreased DM accumulation in the shoot and increased it in the root, decreased RGR, increased specific leaf weight, decreased non-reducing sugar and increased reducing sugar in groundnut seedlings.

The timing of drought has a large impact on the variation. The sensitivity of a genotype to drought increases with yield potential, increasing the closer the drought ends to final harvest. Genotypic variation to drought exists in the water-use ratio with some, being able to accumulate up to 30 per cent more shoot DM with the same total transpiration and HI, and large variations in genotypes to midseason are due to recovery differences after the drought is relieved. Drought stress effects on groundnut depend primarily on the stress pattern because genotypic variation is usually of secondary significance. Pod yield is a function of transpired water (T), transpiration efficiency (TE) and harvest index (H). The yield losses (per cent) due to drought are estimated as: Yield loss (per cent) =  $100(1 - D_y/W_y)$ , where,  $W_y$  is the pod yield under adequate irrigation and  $D_y$  is the pod yield under drought. In most part of India, in a 110-120 days crop water stress at 45-70 DAS (flowering) and pod development (60-90 DAS) phases was highly detrimental to leaf area development, dry matter production, pod formation causing 40-60 and 50-70 per cent yield reductions, respectively and the recovery of growth from water stress was better after relief at the vegetative phase than at later growth phases. However in a 140-150 days crop maximum reduction in kernel yield when stress was imposed during seed filling phase, *i.e.*, 93 DAS onwards.

The water requirement of groundnut varies with the stages and is lowest from germination to flower formation and reaches maximum during pod formation. However, the utilization of available moisture is greatest during flowering and pod formation and the crop receiving adequate water during these stages only can give equal yield to the well watered crop. During these stages if stress is given and later on water supply is resumed only the vegetative growth is benefited not the reproductive growth of crop. Thus the period of maximum sensitivity to drought occurs between 50-80 DAS, the period of maximum flowering and vegetative growth. The yield reductions have been reported to be 10-15, 15-30, 40-50 and 50-70 per cent, respectively when drought was imposed from 10-30, 30-50, 50-80 and 80-120 days after sowing respectively. Yield decreases due to water stress at different growth stages are in order of stress at seed development > at early pod filling > at early growth > at early pegging.

The period of reproductive growth stages occurs over a period of nearly two months and moisture stress has a depressing effect on flowering, stem growth and nodulation. No flowering occurs during the stress, but once the stress is relieved, there is a flush of flowering depending on the growth stages and sometimes it results in more flowers than control. The Virginia type groundnuts, due to their longer duration, are more tolerant to drought than Spanish and Valencia and the Spanish and Valencia due to short duration escape the late season drought. The flush of late flowers following mid season drought delay maturity and hence late harvesting, where late season rain helps. The fruiting occurs once the gynophores enter into the

soil and soil physical condition is important and must be wet during the gynophore entering the soil as the gynophore can exert a force equivalent to 3-4 g only. Under water stress there is poor pod filling that reduced kernel size, shelling, SMK per cent and lipid content of kernel.

Plant population influenced both the temporal and spatial patterns of water use, with high density crops extracting water from lower depths sooner than low density crop. High water use prior to early pod filling in high density crop was associated with more rapid leaf area development. The more rapid water extraction in a high, compared with a low, population density groundnut crop is associated with greater root production at depth.

In order to sustain plant growth and hydration, water must be continuously supplied to the leaves as it is lost by transpiration. This becomes difficult under low soil moisture condition. Some of the management practices avoiding minimizing drought are summarized below:

- ☆ In groundnut, water stress delay pod initiation, and the major cause of variability in pod yield and HI is the delay between peg initiation and onset of rapid pod growth. The management practices should aim to optimize the availability of growth resources at the time of pegging in order to ensure that pod initiation is not delayed.
- ☆ The yield is a function of many plant and environmental factors and moisture stress play an important role particularly the stage at which stress occurs. The water stress affects the vegetative, root and reproductive growth and a proper scheduling of irrigation is required.
- ☆ Moisture stress at flowering reduced phytobiomass and pod yield by limiting the number of mature pods per unit area as compared to stress at pegging and pod formation stages. The variation in HI account for the large proportion of variation in yield, and hence recommended to make selection for high HI.
- ☆ As reproductive development is sensitive to drought resulting to poor yield, the strategies to combat drought in groundnut genotypes are (i) early production of flowers, pegs, and pods, with subsequent filling of the pods at a moderate, but essentially at constant rate despite the drought, (ii) faster development of later developed pegs into pods once water become available after drought late in the season.
- ☆ The early and continuous availability of water until the start of pod filling result in large canopy and during the period of drought stress the transpirational demand increases. The transient soil-moisture-deficit stress for 20-25 days as pre-flowering drought during vegetative phase (20-45 DAS) results in synchronized flowering, increases 10-20 per cent pod yield and save 10-15 per cent water mainly due to promotion of root growth during water stress and inhibition of number of vegetative sites (leaves and branches).
- ☆ About 500 mm of water is necessary to produce a crop of seeds with high potential for germination and seedling vigor and pod yield and quality of

groundnut are reduced when less than 300 mm water was received. Groundnut cultivation may be planned accordingly.

- ☆ Drought stress and soil temperature influence maturation rate and thus had an indirect effect on postharvest quality. The greatest yield reduction corresponds to, peak flowering to early pod filling stage and adequate moisture during this period is critical for maximum yield.
- ☆ As gypsum increase early pod development, it provides an escape mechanism from drought. Gypsum applied at flowering increased yield of genotype subjected to drought.

Genetic improvement of crop resistance to drought stress is one component and will provide a good perspective on the efficacy of control strategy through genetic improvement. Selection for drought adaptation under rainfed conditions, though commonly practiced, could be misleading, since it may not reflect the ability of the genotype if the stress occurs during the critical stages of plant development. More efficient selection would require simulated drought conditions, and the use of other indirect selection methods that give a good indication of drought adaptation. Water deficit during seed filling phase, genotypic yield potential accounted for approximately 90 per cent of the variation in pod yield sensitivity to water deficit, and it is unlikely that breeders will be able to combine high yield potential with low sensitivity to drought spanning the seed filling phase, therefore other important strategies are necessary. The pod yield potential accounted for less of the variation in drought sensitivity (15-64 per cent) in the early and mid-season droughts. For these circumstances it may be possible to identify genotypes with both high yield potential and relatively low drought sensitivity.

Seed composition changes dramatically as the crop matures but has relation with environment. Agrometeorological relationship between environment, crop phenology, maturity, and postharvest quality is essential as postharvest quality of groundnut is the resultant of the particular set of environmental and cultural practices during pod growth and maturation. A biochemical basis exists for inferior quality in immature groundnut. The pod yield and quality of groundnut are reduced when less than 30 cm water was received by the crop. Water deficit during seed production affected  $C_2H_2$  and  $CO_2$  production during subsequent germination. Water stress at pod initiation and development phase reduced germinability, vigour, seed membrane integrity thus water deficit during seed development affects subsequent growth of seedlings and could pose a problem in establishment for the succeeding crop. A minimum of 500 mm of water is necessary to produce a crop of seeds with high potential for germination and high proportion of vigorous seedlings. Many a time the superiority of genotype with high yield, in water stress is not reflected in their ancillary characters. *Aspergillus flavus* invasion and aflatoxin contamination in groundnuts are related to drought stress, soil temperature and maturity and small, immature seeds are more likely to be contaminated with *A. flavus* than larger, mature seeds.

Most breeding programmes in groundnut follow an empirical approach to drought resistance breeding, largely based on kernel yield and traits of local adaptation,

resulting in slow progress. Recent use of easily measurable surrogate traits associated with drought tolerance encouraged breeders to integrate these in their selection schemes. However, there has been no direct comparison of the relative efficiency of a physiological trait-based selection approach (Tr) vis-a-vis an empirical approach (E) to ascertain the benefits of the former. The drought tolerance contributing factors in groundnuts are: an extensive root system established before maximum leaf area to meet the transpirational demand, recurrent and synchronized flowering once stress was relieved, water storage cells in the abaxial side of the leaves to provide water when transpiration was greater than the roots extraction of soil moisture; leaf folding during stress to reduce solar incidence; and transpiration regulated by high stomatal resistance during stress.

In groundnuts drought-stress effects depend primarily on the stress pattern because genotypic variation is usually of secondary significance. The different responses of groundnut cv. to drought when assessed relative to the mean response of all genotypes to drought as two major aspects of drought (duration, intensity, and timing relative to crop phenophases) may vary independently. The timing of drought has a large impact on the variation about the mean response. The sensitivity of a genotype to drought increases with yield potential, increasing the closer the drought ends to final harvest. Genotypic variation in response to drought exists in the water-use ratio of genotypes, with some being able to accumulate up to 30 per cent more shoot DM than others with the same total transpiration.

To ensure survival of crops from water deficit and sustainable production stress resistance may involve avoidance mechanisms preventing exposure to stress, tolerance mechanisms permitting the plant to withstand stress through osmotic adjustment, and acclimation by altering their physiology in response to stress. Innovative biotechnological approaches have enhanced our understanding of the processes underlying plant responses to drought at the molecular and whole plant levels. Hundreds of drought stress-induced genes have been identified and some of these have been cloned. Plant genetic engineering and molecular marker approaches allow the development of drought-tolerant germplasm.

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