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Physiological responses of groundnut (*Arachis hypogea* L.) to drought stress and its amelioration: a critical review

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Abstract

Groundnut (*Arachis hypogea* L.), is an important legume cash crop for the tropical farmers and its seeds contain high amounts of edible oil (43–55%) and protein (25–28%). Even though it is a fairly drought-tolerant, production fluctuates considerably as a result of rainfall variability. To develop a water stress response function in groundnut, research works have been done to improve the performance under varying degrees of stress at various physiological stages of crop growth. This review summarizes recent information on drought resistance characteristics of groundnut with a view toward developing appropriate genetic enhancement strategies for water-limited environments. It is suggested that there are considerable gains to be made in increasing yield and stabilizing the yield in environments characterized by terminal drought stress and by shortening crop duration. Many traits conferring dehydration avoidance and dehydration tolerance are available, but integrated traits, expressing at a high level of organization are suggested to be more useful in crop improvement programs. Possible genetic improvement strategies are outlined, ranging from empirical selection for yield in drought environments to a physiological–genetic approach. It was also suggested that in view of recent advances in understanding drought resistance mechanisms, the later strategy is becoming more feasible. It is summarized that application of knowledge into practice in a systematic manner can lead to significant gains in yield and yield stability of the world's groundnuts production. Research is needed to develop transferable technology to help farmers of arid and semi-arid regions. Increasing soil moisture storage by soil profile management and nutrient management for quick recovery from drought are some of the areas that need to be explored further.

Introduction

Groundnut (*Arachis hypogea* L.) is an important oilseed crop as its seed contains 44–56% oil and 22–30% protein on a dry seed basis (Savage and Keenam 1994). Groundnut is grown on 19.3 million ha of land area in about 82 countries. More than half of the production area is in arid and semi-arid regions. Groundnut is frequently subjected to drought stresses of different duration and intensities. Groundnut acreage has fallen by 25.8% in South Africa and 18.5% in east Africa in 1980s compared with 1970s. One of the reasons for the reduction in area and productivity in these areas is drought. (Mahmoud et al. 1992; Fletcher et al. 1992). In India, groundnut yields fluctuated from 550 to 1100 kg ha^{-1} in different years and consequently the total production of the country also varied from 4.3 to 9.6 million tons (Patel 1988). The rise and fall in the yield and production coincided with the percentage deviation from the mean annual rainfall (DES 1990). Early maturing and disease and drought tolerant cultivars have great promise in improving production in semi-arid regions of tropical Africa and Asia. Although numerous studies have been conducted on groundnut tolerance to drought stress, however, no critical reviews have been written since 1990 on the effects of drought stress tolerance of groundnut and its amelioration. The existing literature on drought stress and its amelioration was reviewed to asses the present position, to identify gaps in research and to suggest future research needs. This review provides an overview of present understanding of drought response of groundnut and summarizes current research on the enhancement of the growth and yield ability currently unrecognized in water-limited environments. In the process, strategies used previously to achieve progress in drought environments are analyzed, improvements were proposed, and attempts have been made to assess the potential impacts of current research endeavors.

Drought and rainfall pattern in groundnut growing areas

India ranks first in annual total production (5.5–8.0 million tons) and area (7–8 million hectares) planted to groundnut. Other important countries in the order of their production are China, USA, Indonesia, Senegal, Nigeria, Myanmar, Sudan, and Argentina (FAO 2000). While the area and production of groundnut have been increasing in the world, however, the total productivity remained almost constant (Patel and Golakiya 1988). This is because, rainfall plays an important role in groundnut production in many countries (Boote and Ketring 1990). Low rainfall and prolonged dry spells during the crop growth period are the main reasons for low average yields in India. Zeyong (1992) reported that drought is the most important constraint to groundnut production in China, especially in parts of the northern region where rainfall is less than 500 mm yr^{-1}. Average yield in Australia was approximately 1250 kg ha^{-1}; however, there are reports of yields exceeding 6000 kg ha^{-1} (Middleton 1980). Naing (1980) reported that rainfall was the main factor determining yield in Myanmar. The crop is grown in Sudan on low fertility sandy soils, mostly under low and erratic rainfall with frequent droughts. Other African countries also have considerable area under rainfed conditions and the crop is subjected to periodic drought. The groundnut growing regions of Argentina are in a semi-arid zone and there is also great variability in the time, amount and distribution of rainfall (Pietrarelli 1980). Hamat and Noor (1980) reported that rainfall was sufficient for growth of groundnut in Malaysia which has an equatorial-type climate, characterized by humidity above 60%, abundant rainfall (2000–3000 mm yr^{-1}), and temperature ranging from 22 to 31 °C throughout the year. In Thailand, groundnut is grown in both the dry and wet seasons and the monsoon or wet season begins in May and ends in October. This is the critical time for Thai farmers since about 80% of the total cultivated land depends mainly on rainfall (Lapang et al. 1980)

Effect of drought stress on plant growth and yield

Drought stress has adverse influence on water relations (Babu and Rao 1983), photosynthesis (Bhagsari et al. 1976), mineral nutrition, metabolism, growth and yield of groundnut (Suther and Patel 1992). In addition, drought conditions influence the growth of weeds, agronomic management and nature and intensity of insects, pests and diseases (Wightman and Wightman 1994; Wheatley et al. 1989).

Water relations

Relative water content (RWC), leaf water potential (ψ_L), stomatal resistance, rate of transpiration, leaf temperature and canopy temperature are important parameters that influence water relations in groundnut. RWC of leaves is higher in the initial stages of leaf development and declines as the dry matter accumulates and leaf matures (Jain et al. 1997). Obviously, stressed plants have lower RWC than non-stressed plants. RWC of non-stressed plants range from 85 to 90%, while in drought stressed plants; it may be as low as 30% (Babu and Rao 1983). ψ_L of groundnut leaves show large diurnal variation with high values in the morning when solar radiation and vapor pressure deficits are low, followed by low values around midday and gradually rises after midday (Erickson and Ketring 1985). Osmotic potential follows the same pattern but ranges less widely than leaf water potential. Leaf and canopy temperature of irrigated plants is generally equal to or less than ambient air temperature but rainfed plants often have a higher canopy temperature than ambient air temperature. Transpiration rate generally correlates to the incident solar radiation under sufficient water availability. However, drought stressed plants transpire less than unstressed plants. The same pattern was observed for stomatal conductance (Mohandas et al. 1989).

Black et al. (1985) recorded lower leaf water potential, turgor potential and stomatal conductance when moisture stress was imposed, however, stomatal conductance was more strongly affected than leaf water status. Stomatal conductance was poorly correlated with leaf water potential and soil water potential. The conservative influence of decreased stomatal conductance in non-irrigated plants was negated by increases in leaf-to-air vapor pressure difference caused by associated higher leaf temperatures (Craufurad et al. 2000). Transpiration rates were therefore, similar in both treatments and the lower total water use of the unirrigated stand resulted entirely from its smaller leaf area index. ψ_L of frequently irrigated groundnut is less than -1.2 to -1.3 MPa while stressed plants have leaf water potentials of -3.0 to -5.0 MPa (Bennett et al. 1984; Boote and Ketring 1990).

Subramaniam and Maheswari (1990) reported that leaf water potential, transpiration rate and photosynthetic rate decreased progressively with increasing duration of water stress indicating that plants under mild stress were postponing tissue dehydration. Stomatal conductance decreased almost steadily during the stress period indicating that stomatal conductance was more sensitive than transpiration during the initial stress period. Stirling et al. (1989) found that leaves exhibited marked diurnal variation in leaf turgor while pegs showed less variation and maintained much higher turgor levels largely because of their lower solute potentials. Marked osmotic adjustment occurred in growing leaves but not in mature ones, allowing them to maintain higher turgor during periods of severe stress. This adjustment was rapidly lost when stress was released (Ali Ahmad and Basha 1998). Bhagsari et al. (1976) reported that water potential of leaves and immature fruits were similar under drought stress conditions. It is a general observation that under severe moisture stress conditions, young pods lose their turgor and shrivel.

Azam Ali (1984) reported that stomatal resistance of older leaves was greater than that of younger leaves. The average stomatal resistance was 2.4 s cm^{-1} during pod development and increased to more than 10 s cm^{-1} when moisture stress was imposed. Boundary layer resistance was between 0.26 and 0.48 s cm^{-1} with a mean of 0.34 s cm^{-1}. Transpiration per unit leaf area was more influenced by stomatal resistance and the vapor pressure difference between the leaf and the air than by boundary layer resistance. Leaf area index affected the transpiration per unit land area more than any other factor. Babu and Rao (1983) examined drought stress effects on groundnut over 35 days from 20 to 55 days after sowing. Under adequate water availability, the leaf water potential varied between -0.15 and -1.15 MPa at 6.00 AM and 4.00 PM, respectively. The relative water content ranged between 100 and 87% on the first day of stress imposition. At the end of this 35-day dry period the plants were wilted and leaf water potential was -5.0 MPa. The lowest relative water content recorded was 29.7%. The leaf water potential and relative water content were negatively correlated with a correlation coefficient of -0.95. The linear regression equation was $\psi_L = 64.8–0.61$ RWC. Babu and Rao (1983) also stated that groundnut has the ability to recover from prolonged desiccation (to a level of about -5.0 MPa leaf water potential) indicative of moisture stress endurance. They inferred that the threshold for stomatal closure due to moisture stress in the groundnut appears to be about -1.35 MPa of leaf water potential. Stomata are present on both sides of the leaf (amphistomatous). The upper surface has a mean stomatal number of 243 mm^{-2} in cultivar J-11 (Babu and Rao 1983). Collino et al. (2001a,b) also confirmed that the stomatal frequency was less on the lower epidermis.

Photosynthesis

Canopy photosynthesis is reduced by moisture stress due to reduced stomatal conductance and reductions in leaf area. As moisture stress increases, stomata start closing as a mechanism to reduce transpiration. As a consequence, the entry of carbon dioxide is also reduced. The decrease in conductance of mesophyll cells due to moisture stress results in low conductance of carbon dioxide and a reduction in photosynthesis. Bhagsari et al. (1976) observed large reductions in photosynthesis and stomatal conductance as the relative water content of groundnut leaves decreased from 80 to 75%. The main effect of a soil water deficit on leaf carbon exchange rate is exerted through stomatal closure. They reported reduced carbon exchange rate, decreased transpiration and increased stomatal resistance within 3 days of withholding water in potted plants. Under field conditions, Allen et al. (1976) found reduced stomatal resistance by 7 days after stress and significant differences within ten days between stressed and non-stressed plants. The long-term effect of soil water deficit on canopy assimilation is a reduction in leaf area. Leaf expansion is more sensitive to soil water deficit than stomatal closure (Black et al. 1985). Drought reduces leaf area by slowing leaf expansion and reducing the supply of carbohydrates.

Reddy and Rao (1968) reported that severe drought stress decreased the levels of chlorophyll *a*, *b* and total chlorophyll. The decrease in chlorophyll was attributed to the inhibition of chlorophyll synthesis as well as to accelerated turnover of chlorophyll already present. However, mild drought stress increased the chlorophyll content (Moreshat et al. 1996). Stirling et al. (1989) reported that leaves were the primary sites of ^{14}C fixation, followed by stems and pegs. Fixation of carbon was low during drought stress but increased sharply when drought stress was relieved. Under drought stress, stems were initially the major sinks for carbon-dioxide but their sink activity disappeared almost completely when stress was ameliorated. Dry matter accumulation is reduced by prolonged water deficit (Rao et al. 1985; Sivakumar and Sharma 1986).

Carbon dioxide

The effect of elevated atmospheric CO_2, alone or in combination with drought stresses, on stomatal frequency in groundnut was investigated by Clifford et al. (1995). CO_2 exerted significant effects on stomatal frequency only in irrigated plants. In droughted plants stomatal frequency was reduced by eight percent on the adaxial leaf surface only (Azam Ali 1995). It was suggested that the effects of future increases in atmospheric CO_2 concentration on stomatal frequency in groundnut are likely to be small, especially under conditions of water stress. However, the combination of reductions in leaf conductance and enhanced assimilation at elevated CO_2 will be important in semi-arid regions. It was also demonstrated by Clifford et al. (1993) that elevated CO_2 increased the maximum rate of net photosynthesis by up to 40% in well-irrigated conditions, and by up to 94% on a soil profile. Harvest index was unaffected by elevated CO_2 (Clifford et al. 1993). The primary effects of elevated CO_2 on growth and yields were mediated by an increase in radiation use efficiency and prolonged maintenance of higher leaf water potential during drought.

Anatomical changes

Periodic water stress leads to anatomical changes such as a decrease in size of cells and intercellular spaces, thicker cell walls and greater development of epidermal tissue. The ratio of stomata per epidermal cell is predetermined, but the size of cells is reduced without a reduction in this ratio. Therefore, stomata per unit leaf area tends to increase under water stress. Leaves also become thicker under moderate drought stress (Reddy and Rao 1968). The developing leaves of groundnut have an unusual thick layer of cells devoid of chloroplasts with lower epidermis below the sponge parenchyma. Cells of this layer are considered to be water storage cells (Reddy and Rao 1968). During moisture stress, the opposing leaflets of trifoliate leaf come together and orient themselves parallel to incident solar radiation, in an effort to reduce solar radiation load on the leaf. These parahelionastic movements are common to other leguminous plants. During these movements, the upper photosynthetically active laminar regions of two opposing leaflets come together and the lower surface of the leaflets (with their disintegrated cellular layer beneath the lower epidermis) become exposed to the sky and ground radiation (Chung et al. 1997). These air-filled lower surfaces with their lower conductivity and larger vapor diffusion path are expected to have higher stomatal resistance relative to the upper photosynthetically active layer of the leaflet. These lower surfaces also exhibit radiation reflectance properties (Babu and Rao 1983).

Mineral nutrition and salinity

Nitrogen fixation by leguminous plants is reduced by moisture stress due to a reduction in leghaemoglobin in nodules, specific nodule activity and number of nodules. In addition, dry weight of nodules is significantly reduced in moisture stressed plants. Moisture stress also delays nodule formation in leguminous crops (Reddi and Reddy 1995). There is a considerable amount of evidence to show that N, P and K uptake of groundnut is reduced by moisture stress (Kulkarni et al. 1988). N, P and K uptake and transpiration rate is highly correlated even under mild water stress conditions. Nitrogen assimilation is also affected by moisture stress due to reduction in nitrate reductase activity. There is limited information on the effects of water stress on nodulation and nitrogen fixation in groundnut. Lenka and Mishra (1973) reported fewer (240) nodules per plant when irrigated at 75% depletion of available soil moisture compared to those irrigated at 25% depletion of available soil moisture which had 553 nodules per plant. By contrast, Shimshi et al. (1967) reported no effects of irrigation frequency (7, 14 and 21 days) on nodule number and nodule weight at the end of the season for groundnut grown on deep soil with high organic matter.

Leakage of solutes as a consequence of membrane damage is a common response of groundnut tissue to several types of stresses including low or high temperatures, low soil moisture or high soil salinity. There is much evidence indicating that calcium is required to maintain membrane integrity (Boss and Mott 1980). Chari et al. (1986) reported a favorable influence of calcium additions in crop water relations and tolerance to drought stress in groundnut. Enrichment of tissue with calcium results in maintenance of a higher water status under moisture stress. The extent of membrane damage was reduced when the leaves were subjected to a simulated stress of plants fed with higher levels of Ca^{2+} than leaves without Ca feeding. The rate of water loss from the leaves of Ca^{2+}-enriched tissue was also lower.

Insufficient soil water in the pod zone can depress calcium uptake by developing pods and cause more unfilled pods, single seeded pods and lower calcium content in the shells and seed (Skelton and Shear 1971). Typical symptoms of calcium deficiency in seeds include hollow heart and damage to the embryo or plumule development. These symptoms are more prevalent in pods that are subjected to drought stress during the pod formation period (Wright et al. 1991).

Calcium is supplied to growing fruits of different crops passively through the transpiration stream. Groundnut pods, being underground do not transpire significantly and therefore often do not receive sufficient calcium from xylem flow into the fruit (Skelton and Shear 1971). Growing pods act as roots and absorb soil moisture that is supplied to leaves.

Metabolism

Almost all-metabolic process is affected by water deficits. Severe water deficits cause decreases in enzymatic activity. Complex carbohydrates and proteins are broken down by enzymes into simpler sugars and amino acids, respectively (Pandey et al. 1984). Accumulation of soluble compounds in cells increases osmotic potential and reduces water loss from cells. Proline, an amino acid, accumulates whenever there is moisture stress. Accumulation of proline is greater in the later stages of drought stress and therefore its concentration is considered a good indicator of moisture stress (Reddi and Reddy 1995).

Shoot growth

Water deficits reduce the number of leaves per plant and individual leaf size. Leaf longevity and leaf area duration is reduced by decreasing soil water potential. Leaf area expansion depends on leaf turgor, temperature and assimilate supply for growth, which are all affected by drought. Leaf and stem morphology are altered by water stress. Continuous water deficit results in fewer and smaller leaves, which have smaller and more compact cells and greater specific leaf weight (Chung et al. 1997). Main axis and cotyledonary branches are shorter for water stressed groundnut plants. Soil water deficit reduces internodal length more drastically than node number.

Bell et al. (1993) studied the factors influencing dry matter partitioning in four diverse groundnut cultivars. Rates of dry matter accumulation in pods (pod addition) varied significantly with both cultivar and sowing date. Within cultivars, much of this variation could be attributed to variation in crop growth rate (CGR) during the critical pod addition period. The proportion of current assimilate distribution to pods depended on inherent cultivar characteristics, and also correlated well with current CGR relative to the CGR during pod addition. Assimilate distribution between vegetative and reproductive parts was not influenced by plant density and spatial arrangement of plants. All cultivars appeared capable of remobilizing stored assimilates to maintain near constant rates of dry matter accumulation in pods (Pandey et al. 1984).

Root growth

Roots grow rapidly during germination and seedling stages and within 5 or 6 days after sowing, the taproot may grow 10–16 cm deep and develop a number of lateral roots (Yarbrough 1949). Groundnut roots grow rapidly, consuming a considerable portion of the early-produced assimilates. By 80 days after sowing more than 80% of the total root system is established in long duration varieties (150 days). Ketring and Reid (1993) found that root length density significantly increased at 10 cm depth until 80 days. At 40–45 days, roots had penetrated to a depth of 120 cm and spread laterally at least 46 cm. The investigation of Gregory and Reddy (1982) indicated that the total root length of cultivar Robout 33-1 followed a sigmoid growth curve and peaked at 68 days after sowing.

Root growth of groundnut is influenced by soil moisture. Water stress stimulates the growth of roots into deeper soil (Lenka and Mishra 1973; Narasimham et al. 1977). Allen et al. (1976) concluded from measured soil water extraction that during water stress, roots in lower depths continue to grow deeper even though vegetative growth appears to stop. They further stated that groundnut roots effectively extracted soil water to depths of at least 180 cm in fine sand soil. Simmonds and Ong (1987) found that the cultivar Robut 33-1 more rapidly extracted water from deeper layers when grown at high vapor pressure deficits than when grown in more humid air. Devries et al. (1989) reported that cultivar Florunner had higher root length density in deeper layers (60–150 cm) during drought periods. Florunner exhibited greater capacity for deep rooting at 55 days after sowing than that of soybean or cowpea, especially when grown under drought stress. All these traits contribute to groundnut's ability to avoid drought stress. Pandey et al. 1984) showed that peanut had greater root length density deeper in the soil than other legumes when grown under drought stress.

Sabale and Khuse (1989) observed the highest root lengths when available soil moisture was 80–85% field capacity. They also reported that spraying antitranspirants did not influence either root length or root volume. Fertilizer phosphorus had favorable influence on root volume but not on root length. Meisner (1991) used two non-destructive methods, a rhizotron and minirhizotron to observe groundnut root growth under 30-day drought stress periods beginning 20, 50, 80 and 110 days after sowing. Root growth was reduced significantly by drought stress during 20–50 days after sowing compared with irrigated control in the rhizotron study, however, such differences were not observed in plants grown in minirhizotron (Meisner and Karnok 1991). All other stress periods had no influence on root growth.

Meisner and Karnok (1992) observed root growth on rhizotron glass every week and found that groundnut root system, regardless of water stress, did not exhibit signs of senescence. Root color and florescence of the root system did not change throughout the season at all depths indicating viability of roots. The ability of groundnut to maintain a viable root system during water stress may contribute to the crop's drought resistance (Sanders et al. 1993). Greater carbon partitioning to the root system before pod set, and a root system that maintains itself for a long period should be an advantage over plants whose roots are continually dying and regrowing during reproductive development.

Yield attributes and yield

The start of flowering is not delayed by drought stress (Boote and Ketring 1990). The rate of flower production is reduced by drought stress during flowering but the total number of flowers per plant is not affected due to an increase in the duration of flowering (Gowda and Hegde 1986; Janamatti et al. 1986; Meisner and Karnok 1992). A significant burst in flowering on alleviation of stress is a unique feature in the pattern of flowering under moisture stress, particularly when drought is imposed just prior to reproductive development (Janamatti et al. 1986). When stress is imposed during 30–45 days after sowing the first flush of flowers produced up to 45 days do not form pegs during that time, however, flowers produced after re-watering compensated for this loss (Gowda and Hegde 1986).

Peg elongation, which is turgor dependent, is delayed due to drought stress (Boote and Ketring 1990). Pegs fail to penetrate effectively into air-dry soil, especially in crusted soils. Often, within 4 days of withholding water, the soil surface becomes too dry for peg penetration. Skelton and Shear (1971) reported that adequate root zone moisture could keep pegs alive until pegging zone moisture content is sufficient to allow penetration and initiation of pod development. Once pegs are in the soil, adequate moisture and darkness are needed for pod development. Adequate pod zone moisture is critical for development of pegs into pods and adequate soil water in the root zone cannot compensate for lack of pod zone water for the first 30 days of peg development. After 30 days of adequate pod zone moisture, pods can continue normal growth in dry soil if roots have adequate moisture. Wright et al. (1994) and Bennett et al. (1990) reported that pod formation is affected by a dry pod zone. However, Boote et al. (1992) reported that Florunner and Robout 33-1 produced pods in air-dry soil although at a slower rate. Sexton et al. (1997) has reported that peanut fruit growth is sensitive to surface soil (0–5 cm) conditions due to its subterranean fruiting habit. Dry pegging zone soil delayed pod and seed development. Soil water deficits in the pegging and root zone decreased pod and seed growth rates by approximately 30% and decreased weight per seed from 563 to 428 mg. Peg initiation growth during drought stress demonstrated an ability to suspend development during the period of soil water deficit and to re-initiate pod development after the drought stress was relieved (Sexton et al. 1997)

Pod and kernel development are progressively inhibited by drought stress due to insufficient plant turgor and lack of assimilates. These stages can also be delayed by lack of soil water in the pod zone (Boote and Ketring 1990; Stirling and Black 1991). Pod dry weights were significantly reduced by a 30-day water stress during the pod development stage (Meisner and Karnok 1992). The number of pods per plant can be low due to increases in soil resistance caused by prolonged drought (Sharma and Sivakumar 1991). Drought reduces pod yield primarily by decreasing the duration of the pod development phase (Stirling and Black 1991). Water deficits during kernel or seed development reduce pod and seed weight. Shelling percentage is reduced by moisture stress during seed development (Janamatti et al. 1986).

Prabawo et al. (1990) reported that irrigation applied before and/or after early pod filling stages increased pod yields of Spanish type groundnuts (100-day maturity) to 2.4 t ha^{-1} compared with 0.53 t ha^{-1} in a dryland crop. The dryland crop, which received no rainfall during the season, presumably extracted significant amounts of soil moisture at depths to and below 1.2 m. Pod yield of groundnut and rainfall received during pod formation to maturity were positively correlated in a rainfed crop grown at semi-arid region of Andhra Pradesh in India (Subbaiah et al. 1974). Suther and Patel (1992) found that pod yield was higher with 80% available soil water than with 20% available water. No pods were formed when plants were in water-saturated soil (Bailey and Biosvert 1991). Stirling and Black (1991) concluded that the major cause of variability in pod yield and harvest index in semi-arid tropics was the delay between peg initiation and onset of rapid pod growth. The reason for this is that once pods were initiated, the proportion of dry matter allocated to reproductive sinks was relatively constant.

Moisture sensitive stages

It is essential to identify moisture sensitive developmental stages to minimize damage caused by drought. The pre-flowering phase is less sensitive to moisture stress than the flowering phase. Greater synchrony of pod set in moderately stressed plants during the pre-flowering phase resulted in greater proportion of mature pods at final harvest (Kulkarni et al. 1988; Rao et al. 1988). Yield reductions are greatest with stress imposed during the period between pegging and pod development and lowest with stress imposed from pod development to maturation (Patel and Golakiya 1988). Several reports indicate that the pod development phase is the period most sensitive to moisture deficit (Stirling et al. 1989; Patel and Gangavani 1990; Meisner 1991; Ramachandrappa et al. 1992). Irrigation timing affects pod yield mainly by influencing the duration of pod production. Naveen et al. (1992) found that water stress imposed during the flowering and pegging stages of JL-24 produced the greatest reductions in pod yield followed by water stresses at the early-and late pod stages. In JL-24 the deviation is probably due to the shorter duration of flowering.

Seed viability

Nautiyal et al. (1991) subjected groundnut cultivars to soil moisture stress at different growth stages and reported the moisture stress during the early vegetative phase resulted in an increase of individual seed weight. Stress at pod initiation and pod development stages reduced germination, vigor, seed membrane integrity and embryo RNA content. Moisture stress at pod development resulted in seeds, which, on germination, had low chlorophyll and dehydrogenase activity in cotyledons. Growth potential was linearly related to chlorophyll content and dehydrogenase activity during seed germination.

Quality

Groundnut seed contains approximately 50% oil. Generally, the oleic and linoleic acid together make up 80% of the fatty acids in groundnut oil. Groundnut storage qualities and nutritional quality are both dependent on the relative proportion of saturated and unsaturated fatty acids in the oil. From a human nutritional stand-point, highly polyunsaturated fatty acid content is desirable for lowering plasma cholesterol level. Fats containing a higher percentage of oleic acid are also beneficial in lowering blood cholesterol. The total amount of unsaturation is inversely proportional to the storage life of the oil. Drought stress during the maturation period results in a decreased oleic: linoleic ratio and less stable oil (Hasim et al. 1993). Sharma and Singh (1987) reported that oil content in groundnut cultivar M 13 was not influenced by moisture stress. Conkerton et al. (1989), reported that drought stress early or late in the growing season had little or no effect on seed oil proteins and mineral contents in the eight groundnut varieties tested. Drought during mid-season affected all these components but only the decrease in oil and copper content were consistent for all cultivars.

Pettit et al. (1971) observed that groundnut grown under dryland conditions and subjected to drought, contained more aflatoxin than groundnut grown under irrigation. Wilson and Stansell (1983) reported that water stress during the last 40–75 days of the season contributed to aflatoxin contamination of mature kernels. Sanders et al. (1993) reported that aflatoxin was consistently found in groundnut when pods were exposed to drought stress although roots of these plants were well watered. Generally, aflatoxin was not found in groundnut pods when the pod zone was well watered although root zone was subjected to drought stress conditions.

Pests and diseases

Drought stress has considerable influence on weeds, insect pests, and diseases of groundnut. Drought stress during vegetative growth (up to 30 days after sowing) is considered advantageous. Early drought reduces weed population. In India, after sowing groundnut with a seed drill, the seeds are covered by running a blade harrow to a shallow depth. This operation uproots germinating and germinated weeds as well as loosens the top 3–4 cm of soil. Weeds can not germinate from the topsoil as it gets dried quickly. If a dry period continues for 20–30 days, no weeds will germinate except those from deeper layers.

The degree of insect pest infestation is also affected by drought stress. Wheatley et al. (1989) observed three distinct patterns of the distribution of foliar feeding insects. The leaf minor *Aproaerema modicella* was most densely infected on the most drought stressed plants of groundnut where leaf surface temperatures were highest. The cicadellid *Empoasca kerri* concentrated where there was no drought stress and leaf temperatures were lowest. Thrips were initially more abundant on the plants that were least stressed, but as the condition of the plants worsened, their distribution reversed. Biochemical changes occur in plants when they become drought stressed. These changes include increases in levels of soluble carbohydrates and amino acids in the leaf. These drought-induced changes provide a more favorable diet for insects, especially phloem feeders. Hence the often-observed phenomenon that insects feeding on drought-stressed plants have higher reproductive and development rates. Bud necrosis disease was observed more on drought stressed plants and plant mortality was high due to the disease and insufficiently watered plants.

Indirect influence of drought

Drought is generally accompanied by low relative humidity, high temperature and wind speed which in turn influence groundnut. Simmonds and Ong (1987) found that transpiration of groundnut was strongly influenced by vapor pressure deficit, which typically ranges from 1 to 5 kPa in semi-arid regions. When vapor pressure deficit exceeded 2 kPa, canopy evaporation was restricted. Transpiration rate per unit leaf area increased with increases in vapor pressure deficit implying that any restriction of transpiration through stomatal closure at large vapor pressure deficit was outweighed by steeper vapor pressure gradient from leaf to air.

Developmental processes such as time of flowering, pegging and pod formation were unaffected by different levels of vapor pressure deficits, but the number of branches, flowers and pegs were reduced in the drier treatments. Measurements during the first 30 days showed that in drier environments leaf growth was reduced, and the partitioning of dry matter into roots was enhanced. Under unirrigated conditions, dry matter production in shoots was reduced by 40% compared with well-watered plants as the vapor pressure deficit increased from 1.0 to 3.0 kPa. Growth was reduced by reductions in leaf area, light interception and productivity per unit of light intercepted (Ong et al. 1987; Isoda et al. 1996). Erickson and Ketring (1985) reported that a day temperature of 35 °C reduced individual leaf area and dry weight of well-watered groundnut measured at both 63 and 91 days after sowing. High temperature also reduced total leaf area, number of pegs and seed weight.

Drought stress management

There are several farming practices, operations and actions that could be taken to insure a successful production of groundnut crop under arid and semi-arid conditions. Development of drought resistant varieties by manipulating genotype variations results in higher water user efficiency. In general, the sensitivity of a given genotype to drought increases with increasing yield potential (Narasimham et al. 1977). Genotypic variation also exists in water-use efficiency (WUE, g DM kg^{-1} water) with some cultivars being able to accumulate up to 30% more shoot dry matter than others with the same total transpiration (Williams et al. 1986; Dwivedi et al. 1996; Rucker et al. 1995). Studies conducted at ICRISAT revealed that specific leaf area (SLA) and photosynthetic activity was correlated (ICRISAT 1992). Genotypes with low SLA had high levels of the photosynthetic enzyme ribulose 1–5 bisphosphate carboxylase per unit leaf area, suggesting the enzyme was a major cause for variation in WUE (ICRISAT 1992). WUE and leaf thickness are correlated in groundnut genotypes. Wright and Rao (1992) considered WUE as an important trait for selection of drought resistant varieties. They reported a close and negative relationship between SLA and carbon isotope discrimination (ratios of carbon isotopes $^{13}C/^{12}C$) in leaves. They suggested that the drought resistant genotypes could be selected either by specific leaf area or by carbon isotope discrimination. In their study, the cultivar Tifton 8 had the highest (3.71 g kg^{-1}) and Chico the lowest (1.81 g kg^{-1}) WUE.

Variation in the partitioning of dry matter to pods has been reported (Greenberg et al. 1992) and it was observed that large variation in response of genotypes to midseason drought is due to recovery differences after drought was relieved (Williams 1994). Schilling and Misari (1992) reviewed work done on drought in Senegal and reported four techniques for evaluation of genotypes for drought resistance: protoplasmic resistance to heat and drying, measurement of electrolyte escape, measurement of water loss from detached leaves, and rooting characteristics measured in rhizotron.

Dhopate et al. (1992) reported that cultivar JL-24 was more drought resistant than cultivar TAG-24. The yield reduction due to drought for JL-24 was 32.1% of yield obtained under adequately irrigated conditions while yield reduction was 46.7% for the cultivar TAG-24. Joshi et al. (1988) studied two Spanish bunch cultivars, GG-2 and JL-24, and found that GG-2 had higher RWC before, during and after stress compared with JL-24. Leaf water potential was also significantly lower in GG-2 than JL-24. After re-watering, the leaf water potential returned to close to pre-stress levels in GG-2 while JL-24 did not recover. Generally, drought tolerant cultivars have lower (more negative) water potential but higher RWC. Transpiration rate of GG-2 was twice that of JL-24 both during stress and after stress relief. Koti et al. (1994) found that the genotype Dh-3-30 was more tolerant to drought compared with TMV 2 and had lower transpiration rate and maximum diffusive resistance when stress was imposed by withholding irrigation for 7 days for plants grown in pots during the summer season. However, pod yields of the two varieties did not differ significantly. Four groundnut genotypes grown in medium deep alfisol in central India transpired similar amounts of water (219–228 mm) over the season but produced different amounts of shoot dry matter (389–493 g m^{-2}) (Mathews et al. 1988)). Taproot extension rates were higher for the cultivar Kadiri-3 in the first 32 days after sowing. TMV-2 and Kadiri 3 produced highest pod dry weight compared to NCAC 17090 and EC 76446.

Virginia type cultivars typically have greater water use efficiencies while Spanish and Valencia cultivars are superior in partitioning dry matter to pods (ICRISAT 1992). Genotypes belonging to Virginia bunch and Virginia runner with small and dark leaves are more drought resistant based on wilting score, while the rate of recovery from drought is faster in genotypes belonging to Spanish bunch. However, Erickson and Ketring (1985) suggested that Spanish types are more tolerant to drought than Virginia types under severe stress and high evaporative demand. Drought resistant varieties typically showed smaller decrease in RWC per unit decrease in leaf water potential compared to susceptible cultivars. Osmotic adjustment has been suggested as a mechanism that leads to smaller changes in RWC per unit decrease in leaf water potential and consequently helps to maintain positive turgor potential during water stress. A Spanish type cultivar, Comet, gave significantly higher yield than Florunner (Virginia type) under rainfed conditions. They concluded that the lower leaf water potential, greater change in osmotic potential and higher pod yield of Comet is related to a greater resistance to dehydration when soil moisture deficits and high evaporative demand conditions occur.

Reddy and Setty (1995) reported that ICGS (E)-198 and K-134 are considered to be drought resistant varieties based on wilting score and leaflet angle during drought stress. The rate of recovery after drought stress was faster with TMV2, which grew at 1.66 cm day^{-1} during the first week after stress relief compared to K-134 (0.4 cm day^{-1}). Considering different parameters like growth during drought, rate of recovery after drought, pod yield and haulm yield, ICGV 86699, K-134, and TMV-2 were all considered as drought resistant varieties and suitable for arid regions. Nigam et al. (1991) reported that groundnut cultivar ICGS-1 released from ICRISAT had moderate recovery from mid-season drought. Manoharan et al. (1989) developed VRI-2 from the cross between JL-24 and CO-2. VRI-2 is a drought resistant variety and produces an average pod yield of 1.79 t ha^{-1} under rainfed conditions. Ali and Malik (1992) reported that ICGS (E) 52 and ICGS (E) 56 were promising short duration varieties suitable to the rainfed areas of Pakistan and could escape end of season drought due to their short duration.

Mahmoud et al. (1992) stated that the most important advance in rainfed groundnut research in eastern Africa was the release of the US line EM 9 in 1987 as a new variety, Sodiri, to replace Barberton. In 12 trials over three seasons and four locations, the new variety out yielded Barberton by an average of 20.5%. The new varieties released in Ethiopia were NC 4X, NC 343 and ICG 94. They recorded yield ranging from 2 to 5 t ha^{-1} under rainfed conditions. Schilling and Misari (1992) reported that intensive research done in western African countries resulted in the release of several drought resistant, short duration, and erect growing varieties. The variety 55-437 was released for cultivation in the dry zones of Niger, Nigeria, Chad, Gambia, and Cameroon. SAMNUT-18 is another variety released for the region, which had 55-437 as one of its parents. The other drought resistant varieties released in West Africa are: 73-30, Te-3, Ts-32-1 and 73-73. Drought resistant varieties suitable for Botswana are: 55-437, 73-30, Flower 11, GG 8-35, ICGS (E) 30 and ICGS (E) 60.

Supplemental irrigation

Prolonged dry spells during pod and kernel development stages can cause irrevocable loss in pod yield and one or two supplemental irrigations during these critical stages known to increase yield (Reddi and Reddy 1995). Rainfed crop grown in the arid tropics of Andhra Pradesh, India was given one supplemental irrigation of 5 cm of water during a dry period lasting more than 15 days. One supplemental irrigation of 5 cm during a 25-dry period day after sowing did not influence pod and haulm yields. With the same quantity of irrigation water given during pod development stage increased pod yield by 27% and haulm yield by 24% over control (Reddy 1994; Reddy and Setty 1995). Sharma and Singh (1987) found that the number of gynophores and pods plant^{-1}, 100-seed weight, pod yield and shelling percentage were highest with two supplemental irrigations at 50 and 80 days after sowing and were lowest under rainfed conditions. Irrigation at 80 days after sowing was more effective than irrigation at 50 days. However, oil content was not influenced by moisture stress.

Seed hardening

There are reports of long lasting effects of seed hardening on germination and subsequent growth of groundnut. Arjunan and Srinivasan (1989) found that dry matter accumulation and pod yield depends on the chemicals used for seed hardening and their concentration, which varied between cultivars. In general, seed hardening with 1% calcium chloride or 2% KH_2PO_4 was most effective. However germination was adversely affected by seed treatment with 1.5% succinic acid. Bharambe et al. (1993) found that the hydropholic polymer *Jalasakti* did not influence pod yield either by seed treatment or by soil application.

Plant population

Wright and Bell (1992) reported that a densely planted crop extracted water from lower depths sooner than a low-density crop. Reproductive development was strongly influenced by plant population density, with more pods m^{-2} in low than in high-density crop. Lower leaf water potential and individual leaf photosynthetic rates in the middle of the day during pegging and early podding phases suggest that high crop water deficits lowered assimilate availability and reduced reproductive potential in high compared with low density crops (Funderburk et al. 1998). They suggested that reducing plant density improved pod yield of groundnut grown on residual soil moisture. The irrigation timing of water rather than the total amount of water applied was a major determinant of pod yield. Wright and Bell (1992) reported that dry matter production under moisture stress conditions was maximized at 40000 plants ha^{-1} compared to production in higher plant populations. The short duration Spanish cultivar, McCullin, showed yield response up to 80000 plants ha^{-1} while the Virginia cultivar, Early Bunch was only up to 40000 plants ha^{-1}.

In a very dry season on sandy soils at Sabele, Botswana, yields of a Spanish variety were highest at a density of 166000 plants ha^{-1} and lowest at 37000 plants ha^{-1}.Very low density led to prolonged flowering, uneven maturity, and low shelling percentage (Mayeux and Maphanyane 1989). The optimum populations for Spanish bunch cultivars under rainfed conditions in India is 333000 plants ha^{-1} (NARP 1992). Generally crops grown on residual moisture should be planted at lower populations than those grown during rainy season.

Antitranspirants

Naveen et al. (1992) reported that spraying of 3% kaolin during dry periods at 35 and 55 days after sowing resulted in a 139% yield increase over controls. Naveen et al. (1992) found that spraying of kaolin (3%) reduced the adverse affect of drought on groundnut crop. Spraying of kaolin (5%) during drought stress at its pod development phase increased pod yield over control. Lime, an easily available material, when sprayed at 1% to moisture-stressed plants, gave significantly higher pod yield over control (Reddy 1994; Reddy and Setty 1995).

Conclusions

Literature review on drought stress and its amelioration in groundnut revealed that sufficient information is not available on respiration, nodulation, hormonal relationships and anatomical changes during drought to come at any meaningful conclusion. The response of groundnut flowering to drought is well-studied, but growth of pods under drought stress, their addition, degeneration, and retranslocation of carbohydrate. are not well understood. Similarly, the influences of soil physical conditions on the growth of pods, especially during drought needs further exploration. One-tenth of the area under groundnut is on shallow Affisols whose water-holding capacity is considerably low. Ways to increase water holding capacity requires further study. Reflectant type antitranspirants reflect the entire solar radiation spectrum including photosynthetically active radiation. Materials with reflecting properties in the infrared region of solar radiation may reduce transpiration without reducing yield. Screening of the antitranspirant materials and the feasibility of their application on groundnut should be examined. Detailed studies are necessary to determine the effect of drought stress on nitrogen fixation, and to find methods of supplying nutrients for quick recovery of drought stressed plants. Most drought amelioration measures reported are related to use of antitranspirants, supplemental irrigation and seed hardening. Reflectant type of antitranspirants are only useful as a method of preventing crop death under severe drought but do not increase yield. Supplemental irrigation, if provided at pod development stages, increases yield but availability of water for irrigation is often limited. Seed hardening techniques rarely increase yield more than 10%. Some drought amelioration measures like drought resistant varieties, and nutrient management appear promising. Simple techniques are needed for farmers in economically disadvantaged regions.

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