Chapter two – Effect of Climate Change Factors on Processes of Crop Growth and Development and Yield of Groundnut (Arachis hypogaea L.)

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Abstract

Global warming is changing climate in terms of increased frequency of extreme weather events as well as increased air temperature and vapor pressure deficit of air and spatial and temporal change in rainfall. In spite of beneficial effect of increased atmospheric CO_2 concentration, climate change will adversely impact the production and productivity of groundnut grown in subtropical and tropical regions of the world. The paper reviews the current state of knowledge on effects of climate change factors on the growth and development of groundnut. The review identifies research gaps and suggests upgrades to groundnut models, such as the CROPGRO-Groundnut model, which is being used as a tool to assess impacts of climate change on groundnut crop. The review revealed that the direct and indirect effects of most climate change factors on plant growth and development processes are well understood and already incorporated in the CROPGRO-Groundnut model. Extreme events associated with climate change may sometime cause water-logging, extreme soil water deficiency or extreme humidity conditions, and these effects could be better addressed in the models.

1. INTRODUCTION

The Fourth Assessment report of the Inter-Governmental Panel on Climate Change (IPCC, 2007) has reconfirmed that the atmospheric concentrations of carbon dioxide, methane and nitrous oxide greenhouse gases (GHGs) have increased markedly since 1750. The global increases in CO_2 concentrations are due primarily to fossil-fuel use and land-use change, while those of methane and nitrous oxide are primarily due to agriculture. The IPCC has also shown that these increases in GHGs have resulted in warming of the climate system by 0.74 ^oC over the past 100 years; and the projected increase in temperature by 2100 is about 1.8 to 4.0 ^oC . For the South Asia region, the IPCC has projected 0.5-1.2^o C rise in temperature by 2020, 0.88-3.16 ^oC by 2050 and 1.56-5.44^o C by 2080 depending upon the scenario of future development. Overall, the temperature increases are likely to be much higher in winter season than in rainy season. With climate change, more frequent hot days, heat waves and warm spells are expected to increase. These increases in the temperatures are likely to result in both spatial and temporal variations in rainfall. Overall, there will be increase in rainfall especially in the tropical regions. The pattern of precipitation is already changing and will become more erratic and intense with warming of the globe. Because of increase in temperatures, vapor pressure deficit of the air will increase in spite of increase in humidity with the increase in rainfall. For the A1B SRES scenario, the expected increase in CO_2 concentration will be 420 ppm by 2020, 530 ppm by 2050 and 650 ppm by 2080 as estimated by the SPAM model (IPCC, 2001).

These changes in climatic factors (CO_2, temperature, vapor pressure deficit and rainfall) will alter plant growth and development processes and most likely have negative impact on crop productivity, especially in the semi-arid tropical regions, where the current temperatures are already high and close to the upper limits beyond which the plant processes will be adversely affected. Therefore, in spite of some expected benefits of increased CO_2 concentration on some crops, global warming poses a potential threat to agricultural production and productivity throughout the world. Increased incidence of weeds, pests and plant diseases with climate change may cause even greater economic losses to agricultural production. It is projected that even small rise in temperature (1-2 ^oC) at lower latitudes, especially in the seasonally dry tropical regions (IPCC, 2007) would decrease crop productivity.

Groundnut (*Arachis hypogaea* L.) is one of the major oilseed and food crops grown in subtropical and tropical regions of the world. It is grown in different rainfall and temperature regimes on a variety of soils. Being a C3 crop, higher temperatures and other climatic factors may affect its productivity and to some extent its distribution. This paper attempts to review the current state of knowledge of climate factor effects on growth and development response of groundnut and revisits the need to fine tune the CROPGRO and other groundnut models to determine the impacts and adaptation of groundnut to climate change in future.

2. VEGETATIVE DEVELOPMENT

2.1. Germination and emergence

After groundnut seeds are sown, germination and emergence are primarily determined by the temperature and soil moisture in the seeding zone. The processes of germination and emergence have a minimum threshold value, optimum range and maximum threshold value for both temperature and soil moisture contents. At minimum threshold values of temperature (base temperature) and soil moisture content, the processes of germination are not initiated. At the optimum range of temperature and soil moisture both, germination and emergence takes place at a maximum rate. Between their minimum threshold and lower optimum values, the rates of germination and emergence increase with the increase in temperature and soil moisture. Above their optimum range, these processes are progressively slowed down until they completely stop at their respective maximum threshold values (damaging thresholds). For example, Awal and Ikeda (2002) and Prasad *et al.* (2006) reported that base temperature for germination of groundnut is approximately 10^{o}C and the optimum temperature for emergence is between 25-30^{o}C. Mohamed *et al.* (1988) and Angus *et al.* (1981) reported base temperatures ranging from 8 to 13 ^{o}C for groundnut seed germination. These differences in base temperature suggest genotypic difference among cultivars studied. In terms of soil temperature, the optimum mean soil temperature for seed germination is between 29 and 30 ^{o}C (Mohamed *et al.*, 1988) and for root growth it is close to 30 ^{o}C (Suzuki, 1966). Leong and Ong (1983) also reported that in two cooler (wet) soil

temperatures (19 and 22 ^{o}C) less than 50% emergence of groundnut seedling took place; while at warmer temperatures (25, 28 and 31 ^{o}C) the percentage of emergence varied from 70-80%. Seedling emergence started within five days after sowing (DAS) in warm temperatures but in 10 DAS at 19 ^{o}C.

2.2. Leaf appearance and leaf number

Like germination and emergence, vegetative development of groundnut crop is also determined by temperature and soil moisture availability. As soil moisture availability decreases, turgor pressure in leaves decreases and slows leaf appearance and expansion. There may also be limited variation among genotypes (ecotypes) in response to temperature and soil moisture. Leong and Ong (1983) reported that base temperature, below which there is no development, varied between 8 ^{o}C to 11 ^{o}C among several genotypes. They also reported decrease in leaf appearance rate under water deficit conditions. Bagnall and King (1991a) estimated that Spanish varieties have a phenological base temperature of 13.6 ^{o}C; whereas Valencia and Virginia varieties have a base temperature of 12.6 ^{o}C and 11.4 ^{o}C, respectively. As far as soil temperature is concerned, rate of leaf appearance showed positive linear functions with soil temperatures (Awal and Ikeda 2002). The plants grown in comparatively warmer soil produced more leaves on their branches than on the main axis. This phenomenon of increasing leaf number on branches in warmer soil gives plants the initial vigor for establishment by capturing more light and CO_2. The impact of soil temperature is less at later stages as plants become more dependent on air temperature rather than soil

temperature for their development. Studies on day and night air temperatures showed that optimum temperatures for vegetative development in groundnut range from 25/25 ^{o}C (Wood, 1968) to 30/26 ^{o}C (Cox, 1979). Marshall *et al.* (1992) recorded maximum rate of foliage development for groundnut (cv. Robut 33-1) in the temperature range of 28 ^{o}C to 30 ^{o}C. More recently, Williams and Boote (1995) and Weiss (2000) reported the optimum temperature range from 25 to 30 ^{o}C for vegetative development of groundnut.

Rao (1999) studied the interactions of CO_2 and temperature on groundnut (cv. TMV 2) growth and development using open top chambers. Plants were grown in ambient conditions for 30 days in pots, and then transferred to open top chambers maintained at combinations of two levels of temperature (35 and 40 ^{o}C) and two levels of CO_2 (330 and 660 µmol mol^{-1}). At all temperature and CO_2 levels, the total number of leaves per plant ranged from 33 to 36 per plants at 60 days of plant age. Elevated CO_2 did not significantly change the total leaf numbers, however, leaf area and leaf weights were higher at elevated CO_2 than at ambient CO_2. There was no interaction between CO_2 and temperature for leaf numbers per plant.

3. CANOPY EXPANSION AND GROWTH PROCESSES

3.1. Leaf thickness

Specific leaf area (SLA) influences canopy expansion and growth through its effect on total leaf area per plant affecting light interception and light use efficiency. Temperature is the major factor affecting SLA of groundnut. Ketring (1984) studied the effect of

temperatures ranging from 30/22 to 35/22 ^{o}C on the growth and development of two groundnut cultivars (Tamnut 74 and Starr). Observations made at 63 and 91 days after planting (DAP) showed that SLA of both the cultivars was unaffected over time in growth chambers maintained at 30/22 ^{o}C; whereas at 35/22 ^{o}C the SLA of both the cultivars increased much faster during the same period, cultivar Tamnut 74 being less sensitive than Starr. However, Talwar *et al.* (1999) did not observe any significant effect of temperature increase from 25/25 ^{o}C to 35/25 ^{o}C on the SLA of three cultivars studied. Pilumwong *et al.* (2007) studied the growth and development responses of groundnut cultivar Tainan 9 to the combination of two temperatures (25/15 ^{o}C and 35/25 ^{o}C) and three CO_2 concentrations (400, 600 and 800 µmol mol^{-1}). Observation made at 112 DAP showed that SLA of plants was 22% less at low temperature than at high temperature. Elevated CO_2 did not affect SLA. In an open top chamber study, Rao (1999) did not observe any significant effect of temperature increase from 35 to 40 ^{o}C on SLA of TMV 2 variety. Increase in CO_2 concentration from 330 to 660 µmol mol^{-1} did not affect SLA. In both the studies the interaction between CO_2 and temperature for SLA was non-significant. From these studies, it is clear that SLA of groundnut increases with the increase in temperature. However, different results were obtained in different studies.

3.2. Leaf area and stem elongation

In a growth chamber study Ketring (1984) showed that when groundnut plants were transferred from 30/25 ± 1 ^{o}C to experimental temperatures (30/22, 32/22, and 35/22 ^{o}C) the leaf area of two cultivars (Tamnut 74 and Starr) progressively decreased with the increase in temperature when observed at 63 and 91 DAP. At harvest (91 DAP) the decrease in leaf area per plant was about 49% for Tamnut 74 and about 80% for Starr at 35/22 ^{o}C as compared to leaf area of respective cultivars at 30/22 ^{o}C. Stem elongation was significantly inhibited by both 32/22 ^{o}C and 35/22 ^{o}C for Tamnut 74 and by 35/22 ^{o}C for Starr. Contrary to the Ketring's results, Talwar *et al.* (1999) in a glasshouse study observed that all vegetative growth parameters (such as leaf area, stem elongation etc.) of three genotypes (ICG 1236, ICGS 44 and Chico) increased at 35/25 ^{o}C as compared to those observed at 25/25 ^{o}C. These contradicting results between the two studies may be caused by lower light intensity in growth chamber studies.

In the Rao (1999) study both high temperatures (40 vs. 35 ^{o}C) and high CO_2 (660 vs. 330 µmol mol^{-1}) increased leaf area per plant. Leaf area per plant was maximum in elevated CO_2 at 40 ^{o}C and minimum in ambient CO_2 at 35 ^{o}C. Length of the longest stem in all treatments was not significantly affected by temperature or enrichment of CO_2. Pilumwong *et al.* (2007) in a growth chamber study observed that at 112 DAP, the total plant leaf area decreased with increasing temperature from 25/15 to 35/25 ^{o}C at all levels of CO_2 concentrations. Leaf area per plant averaged over two temperatures was greatest in 600 µmol mol^{-1} CO_2, followed by 800 µmol mol^{-1} CO_2 and 400 µmol mol^{-1} CO_2. The interaction between temperature and CO_2 was not significant for leaf area per

plant. At 25/15 ^{o}C, main stem length was 24 and 44% longer in 600 and 800 µmol mol^{-1} CO_2, respectively, in comparison to plants grown at 400 µmol mol^{-1} CO_2; while at 35/25 ^{o}C the main stem lengths were similar across CO_2 concentrations. These responses of increase in stem length with increasing CO_2 concentration at 25/15 ^{o}C and no significant change at 35/25 ^{o}C might be because of detrimental effect of high temperature in combination with low light on synthesis and translocation of assimilates to plant parts (Pilumwong *et al.,* 2007). The differences in results between the two studies for leaf area and main stem lengths may be due to different experimental set ups for the two studies. Rao (1999) conducted the experiment in an open top chamber, while Pilumwong *et al.* (2007) conducted in controlled growth chamber. However, these studies give an indication that leaf area per plant and stem elongation may increase up to 35 ^{o}C with the increase in temperature.

Clifford *et al.* (1993) studied the growth and yield of groundnut variety Kadiri 3 grown in controlled-environment glasshouses at 28 ^{o}C (± 5^{o}C) under two levels of atmospheric CO_2 (350 ppm or 700 ppm) and two levels of soil moisture (irrigated weekly or no water after 35 DAS). In the irrigated treatment, the maximum leaf area index (LAI) reached 7.5 in ambient CO_2 and 8.0 in elevated CO_2 at the end of the season. Under drought conditions, elevated CO_2 had a highly significant effect on canopy development. Plants achieved maximum LAI of 3 in ambient CO_2 and 4.3 in elevated CO_2. Later when the drought conditions intensified, LAI declined to 1.9 in the ambient CO_2 and 3.0 in the elevated CO_2. Groundnut plants grown under elevated CO_2 in drought conditions

maintained less negative leaf water potential than the plants grown in ambient CO_2, which helped in maintaining turgor potential for growth and expansion of leaves. These results showed that elevated CO_2 benefits the crop growth under both water limiting and non-limiting conditions; however, the relative benefits are more under water limiting conditions (something that model simulations also show).

3.3. Leaf senescence

Hardy and Havelka (1977) reported that CO_2 enriched treatment accelerated the leaf senescence in groundnut plants. In contrast, Chen and Sung (1990) found that groundnut plants grown at two concentrations of CO_2 (1000 μLL^{-1} and ambient 340 μLL^{-1}) had similar timing of start of leaf senescence. The study of Hardy and Havelka (1977) might have had confounding effect of ethylene contamination of CO_2.

3.4. Stomatal conductance and transpiration

In a controlled growth chamber study, Prasad *et al.* (2003) reported that stomatal conductance and transpiration rates significantly increased with the increase in temperature and decreased with the increase in CO_2 concentration. In the temperature range of 32/22 to 44/34 ^oC, stomatal conductance increased linearly by 0.12 and 0.04 mol m^{-2} sec^{-1} and transpiration by 1.4 and 0.8 mmol m^{-2} s^{-1} with every ^oC rise in temperature under both ambient and elevated CO_2, respectively. The interaction

between temperature and CO_2 was also significant ($p = 0.08$) for these processes (Prasad *et al.*, 2003).

Clifford *et al*. (1995) did not observe any significant effect of CO_2 enrichment (700 vs. 375 ppm) on stomatal conductance during early season (up to 28 DAS) when plants were well supplied with water, however, later in the life cycle, conductance was less for CO_2-enriched compared to ambient plants under full irrigation. At 114 DAS under drought, the conductance of droughted plants had fallen to zero under ambient CO_2, whereas measurable conductance was still recorded for the adaxial leaf surface of plants grown at elevated CO_2, which indicates soil water conservation. Elevated CO_2 as compared to the ambient CO_2 decreased stomatal frequency on both the surfaces of leaves up to 16% in the irrigated treatment and by 8% in the droughted plants on the adaxial surface only. However, elevated atmospheric CO_2 promoted larger reduction in leaf conductance than changes in stomatal frequency, indicating partial stomatal closure. These results suggest that the effects of future increase in atmospheric CO_2 concentration on stomatal frequency in groundnut are likely to be small, especially under conditions of water stress, but that combination of associated reductions in leaf conductance at elevated CO_2 will be important in the semi-arid tropics.

Stronach *et al.* (1994) conducted a study on stands of groundnut (cv. Kadiri 3) in controlled environment glasshouses at two mean air temperatures (28 ^oC and 32 ^oC), two atmospheric CO_2 concentrations (375 ppm and 700 ppm) and two soil moisture

regimes (irrigated weekly to field capacity or allowed to dry from 22 days after sowing). Transpiration equivalent (product of accumulated biomass/ transpiration and saturation deficit of air, g kPa kg^{-1}) was calculated using total above and below ground plant biomass. Neither temperature nor soil moisture treatments had any effect on transpiration equivalent. Increase in CO_2 concentration raised transpiration equivalent value from 6.21±0.30 g kPa kg^{-1} to 7.67±0.29 g kPa kg^{-1} in the dry treatment. This increase of 24% is on the order of the change in the water use efficiency as predicted by Morison (1985) for the whole plants, which is of significant importance for crops grown with limited soil water availability.

3.5. Photosynthesis

Talwar *et al.* (1999) recorded higher net photosynthetic rate in three groundnut genotypes grown at 35/30 ^oC as compared to those grown at 25/25 ^oC at 30 and 60 DAS. They also observed genotypic differences in net photosynthesis at both temperatures. In crops like groundnut (C3 crops), Rubisco is not saturated by the current concentration of CO_2 in the atmosphere. So an increase in CO_2 concentration will improve the balance of CO_2 and O_2 at Rubisco site, thus improving the CO_2-Exchange Rate (CER) of the plant by providing more substrate for photosynthesis. Prasad *et al.* (2003) reported that doubling of ambient CO_2 concentration (350 vs. 700 µmol mol^{-1}) enhanced leaf photosynthesis of groundnut by 27% across a range of day-time temperatures (32 to 44 ^oC), but they found no CO_2 by temperature interaction on leaf photosynthesis. On the other hand, some researchers have suggested that optimum

growth temperature for several plants may rise significantly with increasing concentration of atmospheric CO_2 (McMurtrie and Wang, 1993; McMurtrie *et al.,* 1992; Stuhlfauth and Fock, 1990; Berry and Bjorkman, 1980). Long (1991) calculated from well-established plant physiological principles that most C3 plants should increase their optimum temperature for growth by approximately 5^oC with 300 ppm increase in CO_2 concentration. Thus, photosynthetic rates are expected to rise with simultaneous increases in both the CO_2 concentration and canopy temperature as suggested by Idso and Idso (1994).

Clifford *et al.* (1993) reported that under irrigated condition, the maximum rate of net photosynthesis of groundnut increased up to 40% by elevated CO_2 (700 ppm) compared to ambient CO_2. This was also accompanied by increase in light use efficiency (LUE) for biomass production by 30%, from 1.66 to 2.16 g MJ^{-1} in elevated CO_2. Where no irrigation was given after 35 DAS, the increase in LUE was 94%, from 0.64 to 1.24 g MJ^{-1} in elevated CO_2. Such differences in photosynthetic efficiency were also observed in another study by Clifford *et al.* (1995), where under gradual imposition of severe drought, the net photosynthesis increased under enriched CO_2, while it was negative under ambient CO_2 at 114 days after sowing of groundnut crop. At elevated CO_2, plants maintained less negative and higher leaf water potential which enables them to remain active for longer period of time in dry soil conditions (Clifford *et al.,* 1993).

Chen and Sung (1990) reported that leaf CO_2 exchange rate increased with increasing photosynthetic photon flux density (PPFD) in plants grown at 340 and 1000 μL CO_2 L^{-1}. Plants grown in 1000 μL CO_2 L^{-1} had greater leaf CER at all PPFD levels. The apparent maximum quantum yield estimated from the initial slope of the light response curve of high CO_2-grown plants (0.06 μmol CO_2 per μmol quanta) was much higher than that of ambient CO_2-grown plants (0.026 μmol CO_2 per μmol quanta), indicating better efficiency of light utilization by photosynthesis in high CO_2-grown plants. Leaf CER responded to intercellular partial pressure of CO_2 (C_i) in a curvilinear manner with increasing C_i level. Plants grown at 1000 μL CO_2 L^{-1} consistently exhibited a higher leaf CER than the plants grown at 340 μL CO_2 L^{-1}.

3.6. Net assimilation and growth rates

Rao (1999) in his study reported that both high temperatures (40 vs. 35 ^oC) and CO_2 (660 vs. 330 ppm) significantly increased the net assimilation rate (NAR) of groundnut. At 330 ppm CO_2, NAR increased from 4.092 g m^{-2} day^{-1} to 4.328 g m^{-2} day^{-1} with the increase in temperature from 35 ^oC to 40 ^oC. At 660 ppm CO_2 level, it increased from 4.660 g m^{-2} day^{-1} to 4.890 g m^{-2} day^{-1} with the same increase in temperature. Relative growth rate (RGR) showed a similar trend as NAR in response to temperature and CO_2. The interaction between CO_2 and temperature for both NAR and RGR was significant. Greater NAR and RGR in elevated CO_2 are linked to the increase in rate of photosynthesis (Lenssen and Rozema, 1990, Hertog *et al.*, 1993).

Nigam *et al.* (1994) studied the effect of temperature and photoperiod on growth and development of three genotypes of groundnut (TMV 2, NC Ac 17090 and VA 81B). Mean plant growth rate of three genotypes decreased from 87.5 mg pl^{-1} $^{o}Cd^{-1}$ to 52.4 mg pl^{-1} $^{o}Cd^{-1}$ with the increase in temperature from 22/18 ^{o}C to 30/26 ^{o}C. These results are in contrast to the results obtained by Rao (1999) in an open top chamber study. Mean plant growth rate of genotypes was significantly higher in long day (12 h) photoperiod (84.8 mg pl^{-1} $^{o}Cd^{-1}$) than those in short day (9 h) photoperiod (53.8 mg pl^{-1} $^{o}Cd^{-1}$). There was no interaction between photoperiod and temperature for plant growth rate.

4. REPRODUCTIVE DEVELOPMENT AND GROWTH

4.1 Appearance of flowers, pegs and pods

Leong and Ong (1983) reported that flowering at 19, 22, 25, 28 and 31 ^{o}C occurred at 61, 49, 40, 32 and 31 days after sowing (DAS), respectively, in the wet treatment. In the dry treatment, flowering occurred at 56, 43, 37, 31 and 28 DAS in the same order of increasing temperatures. The calculated base temperature for the appearance of flowering was 10.8 ^{o}C. Bagnall and King (1991a) studied the effect of four temperature regimes (24/19, 27/22, 30/25 and 33/28 ^{o}C) on flowering, fruiting and growth of cv. Early Bunch. The lowest temperature regime (24/19 ^{o}C) considerably slowed the appearance of first flower, and subsequent flower and peg production rates were also strongly depressed by low temperature. In the Talwar et al. (1999) study when the

temperatures were increased from 25/25 ºC to 35/30 ºC, the days to first flower appearance decreased from 37 to 31 for ICG 1236, 38 to 33 for ICGS 44 and 33 to 27 days for Chico. Earlier studies (Fortanier 1957, Bolhuis and de Groot 1959) showed that optimum temperature for time to flowering and vegetative growth for different groundnut varieties is in the range of 28-30 ºC. Marshall *et al.* (1992) also reported that the rate of foliage development increased to maximum in this range of temperatures for cv. Robut 33-1.

Pilumwong *et al.* (2007) reported that the duration from planting to first flower was 22 and 34 days at 35/25 ºC and 25/15 ºC, respectively, for both ambient and elevated CO_2. Prasad *et al.* (2003) observed that the duration of groundnut from sowing to flowering at temperatures 32/22, 36/26, 40/30 and 44/34 ºC was 30, 31, 26 and 28 days, respectively, under both ambient (350 µmol mol^{-1}) and elevated CO_2 (700 µmol mol^{-1}). Thus the optimum temperature for flower appearance was 40/30 ºC (35 ºC). High temperature (40/30 ºC and higher) delayed pegging and podding in groundnut, indicating greater sensitivity of pegging and podding than flowering to high temperatures. Duration from flowering to pegging at both 32/22 ºC and 36/26 ºC was about eight days, while at 40/30 ºC it took about 10 days. The time from flowering to podding was about 16 days at 32/22 and 36/26 ºC, while at 40/30 ˚C it was 19 days. Prasad *et al.* (2003) did not observe any affect of enhanced CO_2 on the phenology of groundnut.

Bagnall and King (1991a) reported that at 30/25 ^{o}C, six photoperiod treatments ranging from 10 to 14 hours, had little effect on days to first flower appearance in four groundnut cultivars (2 Spanish and 2 Virginia types). However, flower production was enhanced significantly in short-day photoperiods. To observe the interaction of photoperiod and temperature for flower appearance, two temperature (24/19 ^{o}C and 30/25 ^{o}C) and five photoperiod treatments (11 to 14 hours) were studied on twelve cultivars (four Spanish, three Valencia and five Virginia types). Average daily irradiance at canopy level during this experiment was 13.7 MJ m^{-2}. Bagnall and King (1991a) found no effect of photoperiod or interaction between temperature and photoperiod on the time to flower. They also subjected a similar range of groundnut varieties to two photoperiods (12 and 14 h) and three temperatures regimes (33/28, 27/22 and 21/16 ^{o}C) in winter with an irradiance level of 7.0 MJ m^{-2} d^{-1}. Most of the varieties examined showed a short day photoperiodic response; they flowered faster under short day at higher temperatures (33/22 or 27/22 ^{o}C). At low temperature (21/ 16 ^{o}C), the time to first flower was similar under both short and long days in all varieties. Bagnall and King (1991a) also reported that photon flux density (Q) below 500 µmol m^{-2} s^{-1} considerably slowed down the progress towards flowering at a constant temperature of 30 ^{o}C. At photon flux density (Q) of 500 µmol m^{-2} s^{-1} and higher, different varieties flowered at a particular dry weight (leaf and stem), whereas at low Q plant dry weights were much reduced at the time of flowering. Thus, delay in flowering associated with low Q is correlated with slowing of dry matter production. Under low Q there was evidence of Q x photoperiod interaction for days to first flower.

These studies by Bagnall and King (1991a) indicated that while temperature has a major role in flowering of groundnut, some modulation by photoperiod and irradiance may be needed under certain climatic conditions.

4.2. Rate of flower production

Bagnall and King (1991b) studied the reproductive development of groundnut in the temperature range of 24/19 ^{o}C to 33/28 ^{o}C. Average rate of flower production (per plant) from the first flower appearance to peak flower production was 11 flowers week^{-1} at 33/28 ^{o}C, 7.4 flowers week^{-1} at 30/25 ^{o}C, 6.6 flowers week^{-1} at 27/22 ^{o}C and 1.8 flowers week^{-1} at 24/19 ^{o}C. They observed that total flower and total peg numbers were strongly correlated with vegetative growth, particularly main stem leaf number, at 70 days of sowing. Disregarding the initial vegetative phase to about 12.5 leaves, on an average in all the temperature regimes, 14.7 flowers were formed for every new leaf on the main stem. Similarly, Talwar *et al.* (1999) also reported that flower number per plant increased at high temperature (35/30 ^{o}C) in three genotypes (ICG 1236, ICGS 44 and Chico) compared to 25/25 ^{o}C. Total flower numbers were also correlated with plant dry weight and number of leaves per plant.

Prasad *et al.* (1999a) studied the effect of high temperature on two groundnut cultivars, ICGV 86015 and ICGV 87282. Initially, both cultivars were grown at optimum temperature (OT, 28/22 ^{o}C) and after first appearance of flower bud (21 DAP) half the

plants were transferred to high temperature (HT, 38/22 ^{o}C). Thereafter, the plants were transferred at three day intervals from OT to HT and from HT to OT, up to 46 DAP, giving a total of nine transfer treatments. Plants remained in the new temperature regime for 6 days before being returned to their original regime, where they remained until harvest at 67 DAP. High temperature had a significant effect (P<0.001) on the total flower number in the controls and in the reciprocal transfer treatments. High temperature increased flower production in the HT-control and OT to HT transfer treatments and vice versa in the HT to OT transfer treatments. However, these changes in flower production only occurred 6 d following transfer to HT or OT (P<0.01). During the 6 d OT or HT stress period, temperature had no significant (P<0.35) effect on flower production. These results show that high temperature had no deleterious effect on flower production but these results did not address the effect of high temperature on fruit set. The effect of temperature treatments was similar for both cultivars and there was no temperature x cultivar interaction.

Bagnall and King (1991b) examined two groundnut cultivars (Robut 33-1 and Early Bunch) in long (16 h) and short day (12 h) treatments and found that short days promoted greater flowering numbers in both groundnut cultivars as compared to long-day treatment. Cumulative flower numbers were greater in short-day treatment than in long-day by 70% for Robut 33-1 and 88% for Early Bunch at 30 ^{o}C at 24 days after beginning of flowering. In the same study, they also reported that flower numbers in groundnut variety White Spanish were also influenced by photon flux density (Q)

imposed after first flower appearance. In four treatments of photon flux density *viz*. 400, 550, 700, 1000 µmol m^{-2} s^{-1} from first week to next 17 days of flowering, flower number at 1000 µmol m^{-2} s^{-1} were double that of those plants at 400 µmol m^{-2} s^{-1}. Plants grown at high Q had more plant dry weight than the plants grown at low Q. The ratio of flower number to dry weight suggested that at higher Q there were proportionally more flowers (35%) than at lowest Q.

Lee *et al.* (1972) grew groundnut plants (cv. Starr) in a greenhouse at 30 ^{o}C until beginning of flowering (30 to 35 days of age). At this time, one group of plants was moved to growth room at 95% relative humidity. At 50 days of age, the relative humidity of the growth room was lowered to 50%. A second group of plants at beginning of flowering was placed into a growth room at 50% relative humidity and at 50 days the humidity was raised to 95%. Flowering was stimulated by transfer from low to high humidity and these plants set the largest percentage of pegs. The plants in the high to low humidity transfer had least number of flowers and formed the lowest percentage of pegs. These results indicate that when plants are exposed to high humidity the flower production is increased.

4.3. Pollen production and viability and fruit-set

Prasad *et al.* (1999b) studied the effects of short episodes of heat stress on pollen production and viability and fruit yield. Plants of cultivar ICGV 86015 were grown at a day/night temperature of 28/22 ^{o}C from sowing until nine days after flowering.

Cohorts of plants were then exposed to a factorial combination of four day temperatures (28, 34, 42 and 48 ^{o}C) and two night temperatures (22 and 28 ^{o}C) for 6 days. Thereafter, all plants were maintained at 28/22 ^{o}C until final harvest 9 days later. Both hot days and warm nights had prominent effect on groundnut pollen production and its viability. As the day temperatures increased from 28 to 48 ^{o}C, pollen production and pollen viability reduced by 390 per flower $^{o}C^{-1}$ and 1.9% $^{o}C^{-1}$, respectively. Warmer nights (28 vs. 22 ^{o}C) reduced mean pollen number from 4389 to 2800 per flower and mean pollen viability from 49 to 40%. Reduced fruit set was a consequence of fewer pollen grains and reduced pollen viability. The threshold temperature for pollen production and viability was 34 ^{o}C and there was strong negative linear relationship between both pollen production and viability and accumulated temperature above 34 ^{o}C. Prasad *et al.* (2000a) exposed the groundnut plants for 6 day periods starting 9 days after flowering (DAF) to the day temperature range of 28 to 48 ^{o}C either for whole day (08:00 to 20:00 hr) or for 6 hrs during AM or PM of the day. Along with air temperatures of growth cabinets, floral bud temperatures were continuously measured over a 6-d period. Variation in flower number was quantitatively related to floral bud temperature during the day over the range 28 to 43 ^{o}C. In contrast, floral bud temperatures above 36 ^{o}C during AM and whole day significantly reduced fruit-set (number of pegs and pods), whereas high PM temperature had no effect on fruit set. They recommended that number of pegs and pods per plant can be modeled by combining the response of flower numbers and fruit-set to temperature.

Talwar *et al.* (1997) showed that flower buds of groundnut are sensitive to temperature stress at a phase 3 to 5 d before anthesis, which coincides with microsporogenesis (Xi 1991; Martin *et al,.* 1974). High temperature during microsporogenesis causes low pollen viability, poor anther dehiscence and hence male sterility. This pollen sterility at high temperature may be associated with early degeneration of tapetal layer (Suzuki *et al.,* 2001 and Ahmed *et al.,* 1992) and reduction in carbohydrates in developing pollen (Pressman *et al.,* 2002).

Prasad *et al.* (2003) also studied the season-long effect of super-optimal temperatures (32/22 to 44/34 ^{o}C) and elevated CO_2 (350 vs. 700 µmol mol^{-1}) on reproductive processes of groundnut. Pollen viability decreased with increasing temperature under both ambient (350 µmol mol^{-1}) and elevated CO_2 (700 µmol mol^{-1}) treatments. Pollen viability of the tagged flowers was about 90-95% at 32/22 and 36/26 ^{o}C, but decreased to 68% at 40/30 ^{o}C and zero at 44/34 ^{o}C. Seed set was 70-80% at 32/22 ^{o}C and 36/26 ^{o}C, 50% at 40/30 ^{o}C and zero percent at 44/34 ^{o}C under both ambient and elevated CO_2. There was no effect of CO_2 or interaction between temperature and CO_2 on pollen viability.

4.4. Number of pegs, pods and seeds

Bolhius and Groot (1959) in their study recorded highest number of pegs at 27 or 30 ^{o}C. Bagnall and King (1991b) reported increase in peg numbers when the temperature was increased from 24/19 ^{o}C to 33/28 ^{o}C. Similarly, Talwar *et al.* (1999) reported increase in

peg numbers of groundnut cultivars when temperature was increased from 25/25 ^{o}C to 35/30 ^{o}C, but the pod numbers decreased with the increase in temperature. These results indicate that peg formation is not adversely affected by temperatures up to the range of 33/28 ^{o}C to 35/30 ^{o}C). However, Ketring (1984) in his range of temperatures (30/22, 32/22 and 35/22 ^{o}C) reported a 33% decrease in number of pegs with increasing temperature from 30/22 to 35/22 ^{o}C, but this was in low light chambers.

In the Prasad *et al.* (2003) study both pegging and podding were delayed above the 32/22 to 36/26 ^{o}C temperature range. As the temperatures increased from 32/22 to 44/34 ^{o}C pod number decreased from 353 to 74 m^{-2} under ambient CO_2 (350 µmol mol^{-1}) and from 407 to 116 m^{-2} under elevated CO_2 (700 µmol mol^{-1}). Similarly, with the same temperature increase, seed number decreased from 587 m^{-2} to 43 m^{-2} at ambient CO_2 and 709 m^{-2} to 132 m^{-2} at elevated CO_2. Across all temperatures, elevated CO_2 compared with ambient CO_2 increased pod number by 40% and seed number by 31%. The interaction between temperature and CO_2 for pod and seed number was not significant.

Air and soil temperature both are important factors to determine the yield of groundnut as groundnut flowers develop aerially and pods in the soil. The optimum soil temperature range for pod formation and development is between 31 ^{o}C and 33 ^{o}C and soil temperatures above 33 ^{o}C significantly reduce the number of mature pods and seed yields (Dreyer *et al.,* 1981; Ono, 1979; Ono *et al.,* 1974). However, Golombek and Johansen (1997) found that the greatest number of pods were produced at slightly low

range of mean soil temperatures i.e. between 23 ^{o}C and 29 ^{o}C, while temperatures of 17 ^{o}C and 35 ^{o}C were sub and supra-optimal, respectively. Prasad *et al.* (2000b) studied the individual as well as combined response of air and soil temperature on yield and yield components of groundnut. The effects of high air (38/22 ^{o}C vs. 28/22 ^{o}C) and high soil temperatures (38/30 ^{o}C vs. 26/24 ^{o}C) were imposed from flowering or podding. High air temperature had no significant effect on total flower production but significantly reduced the proportion of flowers setting pegs (fruit-set) and hence the fruit numbers. In contrast, high soil temperature significantly reduced flower production, the proportion of pegs forming pods, and 100-seed weight. The combined treatment of high soil and air temperatures reduced fruit-set and pod weight by 58% and 57% at podding and 49 and 52% at flowering, respectively, indicating high sensitivity to temperatures at podding stage. The effects of high air and soil temperature were mostly additive and without any interaction.

Bell *et al.* (1991) studied the effect of temperature and photoperiod on Spanish, Virginia and Valencia types of groundnut and reported strong photoperiod x temperature interaction for number of pegs and pods produced. Photoperiod did not affect time to first flower, but the number of pegs and pods and total pod weight per plant decreased in long (16 or 17 h) photoperiods. For example, pod numbers of two cultivars, i.e. White Spanish and NC 17090, decreased with increasing photoperiod (17 h vs. 11.9-13.5 h) at two temperatures (33/17 ^{o}C and 33/23 ^{o}C). Similarly, Bagnall and King (1991b) studied the response of groundnut to temperature, photoperiod and irradiance on

flowering and development of pegs and pods. Flower and peg number at 60 to 70 days from emergence were approximately doubled by 12 h days (SD) compared with plants with 16-h days (LD). Peg numbers were highly correlated to flower numbers and their ratio was independent of differing photoperiod treatments, suggesting that there was no major effect of day length on flower abortion. However, the pod number and, therefore, yield was more influenced by photoperiod than was flower or peg formation. Photoperiod induced changes in flower and fruit numbers were independent of growth and plant dry weight. Conversely, temperature and light intensity affected flower numbers and these changes were correlated with growth-related changes in leaf number and plant dry weight.

Leong and Ong (1983) reported that rate of peg and pod formation, mainly controlled by temperature, was not significantly affected by dry or wet soil treatments. However, Rao *et al.* (1985) observed significant yield reductions when water stress was imposed from start of flowering to start of seed growth. They attributed yield reductions due to water deficits in the top 4 to 5 cm of soil that prevented peg and pod development in the dry and hard soil. Similar results have also been obtained in other studies (Matlock *et al.,* 1961; Boote *et al.,* 1976; Pallas *et al.,* 1979; Underwood *et al.,* 1971 and Ono *et al.,* 1974).

4.5. Pod and seed growth rates and their size

Optimum air temperature for pod growth as suggested by various researchers appears to lie between 20-24 ^{o}C (Williams *et al.,* 1975 and Cox 1979). Cox (1979) observed that the individual and total pod weights and the rate of increase in pod weight were greatest at the mean temperature of 23.5 ^{o}C. So partitioning of dry matter to pods would, therefore, be expected to decrease as temperature increases above 24 ^{o}C (Ong 1984). Pilumwong *et al.* (2007) found that as temperature increases from 25/15 to 35/ 25^{o}C, pod dry weight reduced by 50%. Pod weight reduction by high temperature (35/30 vs. 25/25 ^{o}C) was also reported by Talwar *et al.* (1999) for three genotypes.

Nigam *et al.* (1994) reported that temperature had a significant effect (P<0.01) on pod growth rate but there was no overall effect of photoperiod. In the tested genotypes, highest pod growth rate was observed at 26/22 ^{o}C compared to 22/18 ^{o}C and 30/26 ^{o}C. Photoperiod effects on pod growth rate for cvs. TMV 2 and Nc Ac 17090 were not significant in any temperature regimes. On the other hand, significantly greater pod growth rate for VA 81B occurred in long day than in short day 26/22 ^{o}C. The study may provide evidence of genotypic variability for photoperiod x temperature interaction which could influence adaptation for groundnut genotypes to new environments.

5. TOTAL DRY MATTER, POD AND SEED YIELD

Cox (1979) observed that accumulation of top dry weight in early growth was optimum at a weighted mean temperature of 27.5 ^{o}C and no shoot growth was observed at 15.5 ^{o}C indicating positive linear function of growth above 15.5 ^{o}C. But further increase in

temperature above optimum range may decrease dry matter production. Craufurd *et al.* (2002) observed that high temperature (38/22 ^{o}C) significantly (P≤0.001) reduced total dry weight of four groundnut cultivars (ICGV 86015, 796, ICGV 87282 and 47-16) by 20% to 35% as compared to the 28/22 ^{o}C treatment. Similar results were obtained by Prasad *et al.* (2000b) in a poly tunnel study where the groundnut plants exposed to high air (38/22 ^{o}C) and/or high soil temperature (38/30 ^{o}C) significantly reduced total dry matter production, its partitioning to pods and pod yields of groundnut. Cox (1979) reported that temperatures above 26/22 ^{o}C (24 ^{o}C mean temperature) reduced the pod weight per plant. Ong (1984) observed significant reduction in number of subterranean pegs and pods, seed size and seed yield by 30-50% at temperature above 25 ^{o}C.

Using semi-closed chambers, Chen and Sung (1990) exposed peanut plants (cv. Li-Chih-Taze) to enriched CO_2 atmosphere (1000 µL CO_2 L^{-1}) during two different growth periods, i.e., from pod formation (R3 stage) to final harvest (R8 stage) or seed filling (R5 stage) to final harvest. Groundnut plants produced more dry matter accumulation and higher pod yield in the enriched treatment (1000 µmol mol^{-1} CO_2) as compared to the ambient treatment (340 µmol mol^{-1} CO_2). The enrichment-stage effect on these parameters was not significant.

Pilumwong *et al.* (2007) reported that above ground biomass of groundnut was increased by elevated CO_2 (800 vs. 400 µmol mol^{-1}) in both the low (25/15 ^{o}C) and high (35/25 ^{o}C) temperature treatments. Pod dry weight increased with increasing CO_2 at

25/15 °C °C, but was not different among CO_2 levels at 35/25 °C. At 25/15 °C, pod dry weight was 50% higher than at 35/25 °C. Highest above ground biomass production at 35/25 °C, under 800 µmol mol^{-1} CO_2, indicates that the high temperature regime chosen in this study was still in the optimum temperature range for biomass production of groundnut. Rao (1999) reported increased dry weight of shoot in elevated CO_2 (660 vs. 300 ppm) even at 40 °C.

Prasad *et al.* (2003) reported increase in total dry matter production of groundnut with increase in CO_2 between temperatures of 32/22 °C and 40/30 °C. Further increase in temperature to 44/34 °C decreased total dry matter under both ambient (350 µmol mol^{-1}) and elevated CO_2 (700 µmol mol^{-1}). As the temperature increased from 32/22 to 44/34 °C, pod yield decreased by 89% and 87% under ambient and elevated CO_2, respectively. With the same increase in temperature, the seed yield decreased by 90% and 88% under ambient and elevated CO_2, respectively. Temperature and CO_2 effect on total dry matter, pod and seed yields were statistically significant, however, the interaction between temperature and CO_2 for all yields were not significant. On average, total dry matter yield increased by 36% and both pod and seed yields increased by 30% under elevated CO_2 across all the temperature regimes. The study showed that when the groundnut crop is exposed to high temperatures throughout the full season, total dry matter production is reduced at temperatures above 40/30 °C (35 °C), whereas the pod and seed yields are adversely affected above temperatures of 32/22 °C (27 °C). These results differ from the Cox (1979) study results that optimum temperature for dry

matter production ranges from 25 to 30 ^{o}C with a mean of 27.5 ^{o}C, whereas, the pod and seed yields start declining above 24 ^{o}C. The study of Cox (1979) used pot-grown plants at lower light intensity.

Clifford *et al.* (1993) reported that in well-irrigated conditions, elevated CO_2 (700 ppm) increased above-ground dry matter accumulation by an average of 16% over the ambient CO_2 concentration (350 ppm). Droughted plants grown at elevated CO_2 produced more than double the dry matter of plants grown at ambient CO_2. Average increase in pod yield with elevated CO_2 was ≈25%, from 2.73 to 3.42 t ha^{-1} in well-irrigated plots, with a 6-fold increase from 0.22 t ha^{-1} to 1.34 t ha^{-1} in the droughted treatment. The reason for such differential response to CO_2 in two moisture regimes was discussed earlier as a result of CO_2-induced water conservation in the section on stomatal conductance and photosynthesis.

Timing and intensity of water stress can enhance or reduce yield of groundnut. Rao *et al.* (1985) reported that when groundnut plants received 12-15% less water during vegetative growth (or up to start of pegging) pod yields increased by 12-19% compared to the fully irrigated control. Earlier work at ICRISAT (ICRISAT Annual Report, 1981) and Ong (1984) showed similar increase in pod yield under mild water stress during vegetative phase of groundnut. In the Rao *et al.* (1985) study when plants were stressed from start of flowering to start of seed growth, total biomass and pod yield were reduced as much as 50% and 77%, respectively. Greatest reduction in kernel yield

occurred when stress was imposed during the seed-filling phase. As fruit initiation continues even after the start of kernel growth, soil water deficits during pod filling stage reduce both the initiation and development of pods (Matlock *et al.,* 1961; Boote *et al.,* 1976; Pallas *et al.,* 1979; Underwood *et al.,* 1971; Ono *et al.,* 1974).

6. HARVEST INDEX AND SHELLING PERCENTAGE

6.1. Harvest index

Prasad *et al.* (2003) found that pod and seed harvest indices at harvest maturity were significantly affected by temperature, but not by CO_2. As temperatures increased from 32/22 to 44/34 ˚C, pod harvest index decreased from 0.50 to 0.07 and seed harvest index from 0.41 to 0.05, respectively, under both ambient and elevated CO_2. Talwar *et al.* (1999) reported that harvest index decreased significantly at high temperature (35/30 °C) compared to optimum temperature (25/25 °C) and the decrease was more than 59% in all the tested genotypes. Craufurd *et al.* (2002) also reported similar reduction in seed harvest index ranging from 0 to 65% at high temperature (38/22 ^{o}C) for the four cultivars. Temperature had similar effect of reducing the dHI/dt (rate of change in harvest index) for pod and seeds in all genotypes. High temperature had no effect on dHI/dt of moderately heat tolerant genotypes i.e. 796 and 47-16. But in susceptible genotypes, ICGV 86016 and ICGV 87282, the start of pod and seed filling were delayed by 5 to 9 d and dHI/dt was reduced by 20 to 65% at 38/22 ^{o} C. Craufurd *et al.* (2002) concluded that crop models need to account for genotypic differences in high

temperature effect on timing and rate of dHI/dt to successfully simulate yields in warmer climates.

Bell *et al.* (1991) observed that the harvest index (HI) of cvs. White Spanish and NC 17090 decreased under long day (17 h) as compared to the short days (11.9-13.5 h) at both the temperatures, however, the decrease was more at higher temperature (33/23 ^{o}C) than at lower temperature (33/17 ^{o}C). Nigam *et al.* (1994) also reported decrease in partitioning coefficient (pod growth rate/plant growth rate) of three selected genotypes with high temperature and long photoperiod. Flohr *et al.* (1990) suggested that long days increase the thermal time for initiation of pegs and pods, thus resulting in less partitioning of dry matter to these reproductive organs.

Ong (1984) reported that partitioning of dry matter to pods [expressed as pod weight ratio (PWR)] was 0.178 and 0.042 at 25 ^{o}C and 31 ^{o}C, respectively in an irrigated treatment. In the water limited treatment, PWR decreased with increasing water deficit. At 27 ^{o}C, PWR was 0.104 and 0.067 in the wet treatment having saturation vapor pressure deficit (SVPD) of 1.0 and dry treatment with SVPD of 3.0, respectively. Clifford *et al.* (1993) did not observe any marked difference in seed harvest index (HI) of groundnut in two CO_2 treatments (350 ppm and 700 ppm) in irrigated condition, which was 0.20 under ambient CO_2 (350 ppm) and 0.21 under elevated CO_2 (700 ppm). In the drought treatment, HI was 0.05 in ambient CO_2, which increased to 0.15 in elevated CO_2. Similar results were obtained by Stronach *et al.* (1994) on fraction of biomass

partitioning to pods in ambient and elevated CO_2 (375 vs. 700 ppm) in irrigated and drought conditions.

6.2. Shelling percentage

In Prasad *et al.* (2003) study shelling percentage decreased from 82% to 74% (by 0.7 units $^{o}C^{-1}$) as temperature increased from 32/22 to 44/34 ^{o}C under both ambient and elevated CO_2. High temperature decreases the partitioning of dry matter to seeds which results in low shelling percentage (Craufurd *et al.,* 2002). Ketring (1984) reported a 25 and 20% reduction in mature seed weight at 35 ^{o}C compared to 30 ^{o}C for Tamnut 74 and for Starr cultivars, respectively. Similarly, Talwar *et al.* (1999) reported that seed setting and seed weight of three tested genotypes (ICG 1236, ICGS 44 and Chico) were significantly reduced under high temperature 35/30 ^{o}C compared to 25/25 ^{o}C. Shelling percentage was 60-76% at 25/25 °C and 41-62% at 35/30 °C for three genotypes *viz*. ICG 1236, ICGS 44 and Chico. Rao *et al.* (1985) reported decrease in shelling percentage when water stress was imposed during pod-filling stage.

7. ROOT GROWTH AND ROOT TO SHOOT RATIO

7.1. Root growth

In a phytotron experiment, Wood (1968) reported that root dry weights of groundnut plants decreased with increasing day temperatures from 20 ^{o}C to 35 ^{o}C keeping night temperature the same (25 ^{o} C). At 35/25 ^{o}C root dry weight was only 35% of the weight

at 20/25 ^{o}C and the difference was highly significant. In a short-term rhizotron study, Pilumwong *et al.* (2007) reported that total root length and number of roots at 17 DAP were significantly greater in the plants grown at low temperature (25/15 ^{o}C) than those at high temperature (35/25 ^{o}C) in all CO_2 concentrations. However, in the long-term rhizotron study, plants grown at high temperature (35/25 ^{o}C) had significantly greater root number, greater root length and greater root length density at 99 DAP than those at 25/15 ^{o}C. This shows that short-term study in this case does not represent long-term study in terms of high temperature impacts on root growth. In terms of soil temperature, Suzuki (1966) reported optimum temperature close to 30 ^{o}C for root growth.

Chen and Sung (1990), using semi-closed CO_2 enrichment chamber, studied the effect of CO_2 enrichment on the growth of Virginia type groundnut. In the 340 µL CO_2 L^{-1} treatment root dry weight was 2.01-2.33 g $plant^{-1}$. In the enriched treatment (1000 µL CO_2 L^{-1}), root dry weight was 3.28-3.67 g $plant^{-1}$ when applied from pod to harvest and 2.79-3.41 g $plant^{-1}$ when applied from seed filling to harvest stage. Similarly, Rao (1999) using open-top chamber observed increase in dry weight of root with CO_2 enrichment from 330 ppm to 660 ppm at 35 ^{o}C to 40 ^{o}C. Pilumwong *et al.* (2007) in a rhizotron study observed that when CO2 concentration was increased from 400 to 800 µmol mol^{-1} the fibrous root dry weight of groundnut plants increased at 25/15^{o}C but decreased at 35/25^{o}C. Clifford *et al.* (1993) using closed environment glasshouse observed that under ambient (350 ppm) and elevated (700 ppm) CO_2 the dry root weights were 180.2 and

177.3 g m^{-2} in the irrigated treatment and 274.0 and 274.7 g m^{-2} in the drought treatment in the respective CO_2 concentrations. This indicates that root dry weight was unaffected by CO_2 at a given moisture regime, but was increased by drought. These differences in root weight response to CO_2 in different studies may be attributed to the differences in the crop growth facility used for experimentation.

7.2. Root to shoot ratio

Prasad *et al.* (2000b) reported that partitioning of dry matter to root increased when the plants were exposed to high air temperature (38/22 ^oC) at the beginning of flowering. But when the treatment was applied at beginning pod, partitioning of dry matter to root reduced significantly and no change in total dry matter was observed. This difference in dry matter partitioning to root under high temperature at these two stages could be caused by preferential partitioning of dry matter to reproductive organs when stressed at pod formation stage (Yamagata *et al.,* 1987). Prasad *et al.* (2000b) also observed that partitioning of dry matter to roots was greater when plants were grown at high soil temperature (38/30 ^oC vs. 26/24 ^oC) than when grown in high air temperature (38/22 ^oC vs. 28/22 ^oC). Both high air and soil temperatures above 30 ^oC increase dry matter partitioning to roots.

Craufurd *et al.* (2002) in their study on four groundnut cultivars (two Spanish and two Virginia genotypes) found that root-to-shoot ratio of different genotypes was significantly reduced ($p=0.01$) by 20 to 35% at 38/22 ^oC as compared to 28/22 ^oC**.** Rao (1999) did not find any effect of temperature or CO_2 concentration on the root to shoot

ratio. Root to shoot ratio under ambient CO_2 (330 μmol mol^{-1}) was 0.039 at 35 ^oC and 0.037 at 40 ^oC. Under elevated CO_2 (660 μmol mol^{-1}), it was 0.038 at both the temperatures.

Root-to-shoot ratio considerably decreased under elevated CO_2 (700 ppm) in both irrigated and drought treatments (Clifford *et al.,* 1993). In irrigated treatment, root-to-shoot was decreased from 0.19 to 0.12 when CO_2 concentration increased from 330 ppm to 700 ppm. In the drought treatment, it decreased from 0.70 to 0.33 in respective concentrations of CO_2. Overall, in drought treatment root-to-shoot ratio was greater than irrigated treatments (Clifford *et al.,* 1993).

8. SYNTHESIS OF THE REVIEW FOR IMPROVING THE CROPGRO OR OTHER MODELS FOR GROUNDNUT

8.1. Vegetative development

Base temperature for germination of groundnut seeds is 10 ^{o}C and the optimum temperature for emergence ranges from 25 and 30^{o}C (Awal and Ikeda 2002 and Prasad *et al.,* 2006). However, different genotypes may have different base temperature ranging from 8 to 13 ^{o}C (Leong and Ong, 1983 and Mohamed *et al.,* 1988). Optimum soil temperature for germination is 29 to 30 ^{o}C (Mohamed *et al.,* 1988). Base temperature for vegetative development of groundnut genotypes ranges from 8 to 11 ^{o}C (Leong and Ong, 1983) and the optimum temperature is between 25 to 30 ^{o}C (Williams and Boote, 1995 and Weiss, 2000). Elevated CO_2 does not effect vegetative progression of groundnut (Rao, 1999).

Currently in the groundnut model (Boote *et al.,* 1986, 1991, 1998; Singh *et al*., 1994a, 1994b), the base temperature is 11 ^{o}C and the optimum temperatures for vegetative development range from 28 to 30 ^{o}C, and the damaging threshold temperature is taken as 55 ^{o}C. There is little information in the literature on how vegetative development is affected by temperatures above 30 ^{o}C. Soil temperature and soil water status are considered in the model for germination and emergence, but only air temperature (not soil) is used for subsequent vegetative development. Less is known how soil moisture stress, especially excess soil water, affects the groundnut crop and what is the optimum

range or threshold values affecting germination or vegetative development of groundnut. Extreme events associated with climate change may cause water-logging or extreme soil water deficiency and these effects, if sufficiently understood, need to be incorporated in the model.

8.2. Reproductive progression

Base temperature for first flower appearance is 10.8 ^{o}C (Leong and Ong, 1983) and the optimum temperature is in the range of 28-30 ^{o}C (Fortanier, 1957 and Bolhuis and de Groot 1959). On the other hand, Prasad *et al. (*2003) reported that appearance of flowers was hastened with the increasing temperatures up to 40/30 ^{o}C (35 ^{o}C) but slowed down beyond this temperature. Temperatures above 36/26 ^{o}C (31.5 ^{o}C) delayed pegging and podding in groundnut. Thus, high temperatures increase rate of flowering and flower production, but have deleterious effect on fruit set. At high irradiance level, day length has no effect on days to flower. At low irradiance level, short days enhance time to first flower at high temperatures but not at low temperatures. Low photon flux density (Q < 500 µmol m^{-2} s^{-1}) slows the progress towards flowering and the interaction between Q and photoperiod was significant for days to first flower (Bagnall and King, 1991a). Soil moisture regime or CO_2 concentration does not influence the appearance of flowers in groundnut.

Currently in the groundnut model (Boote *et al.,* 1998), the base temperature for progression to flowering is 11 ^{o}C and the optimum temperature range is 28 to 30 ^{o}C,

with progressively slower progress above 30 ^{o}C, reaching zero progress (damaging threshold) at 55 ^{o}C. In the model, after the beginning seed stage (R5 stage), the base temperature for development is reduced to 5 ^{o}C and the optimum to 26 ^{o}C. There is no short day photoperiod effect for any cultivar currently used in the groundnut model but the code is programmed to accept a short-day sensitivity, if sufficient evidence is provided. So far, none of the 30 or so commonly-grown cultivars exhibit any short-day acceleration of time to flower (we think NC 17090 is not typical of current cultivars). Low Q effect on time to flower is not incorporated in the model, although it could be important for low-light growth cabinets.

8.3. Vegetative expansion and photosynthesis processes

Leaf area expansion and stem elongation increase with the increase in temperature up to 35/25 ^{o}C (Talwar *et al*., 1999). Drought reduces leaf extension rates. Elevated CO_2 benefits the crop growth under both water limiting and non-limiting conditions; however, the relative benefits are more under water limiting conditions (Clifford *et al*., 1993). Threshold temperature up to which SLA increases appears to be 30 ^{o}C. Elevated CO_2 does not influence SLA of groundnut (Ketring, 1984 and Pilumwong *et al*., 2007). Stomatal conductance and transpiration rates increase with temperature, whereas elevated CO_2 reduces these processes. Elevated CO_2 enhances CER, photosynthesis, light use efficiency and transpiration efficiency of groundnut (Prasad *et al*., 2003; Clifford *et al*., 1993 and Chen and Sung, 1990). Talwar *et al*. (1999) observed increase in

crop growth and net photosynthesis when temperature increased from 25/25 to 35/25 ^{o}C, whereas, Bell *et al.* (1991) observed increase in **c**rop growth rates up to 33/23 ^{o}C. Rao (1999) reported that increase in temperature (35 to 40 ^{o}C) and elevated CO_2 (330 to 660 μmol mol^{-1}) had positive effect on relative growth rate (RGR).

In the CROPGRO-Groundnut model (Boote *et al.,* 1998), the expansion processes for plant height and width are decreased at temperatures below 26 ^{o}C. The model reduces leaf expansive processes, e.g. SLA, when temperature falls below the 27 ^{o}C optimum, being reduced to 20% of optimum at 14 ^{o}C. Thus these expansive processes are sufficiently represented in the model. Exact cardinal temperatures for crop growth rate and biomass increase are more difficult to interpret because leaf appearance rate, leaf area expansion, as well as leaf photosynthesis have separate effects, and maintenance respiration increases with rising temperature (in the model). Leaf photosynthesis in the model has an electron-transport rate that has a linear response from zero rate at 8 ^{o}C up to optimum at 40 ^{o}C, but the rubisco competition for CO_2 versus O_2 is programmed in the code and causes quantum efficiency to be reduced as temperature rises, thus single leaf photosynthesis is practically at its maximum between 30 to 40 ^{o}C (Boote and Pickering, 1994). There is also a minimum night temperature effect that reduces light-saturated rate if the minimum temperature is less than 22 ^{o}C. All the processes of CO_2 and temperature sensitivity of photosynthesis are represented in the model directly or indirectly (see method in Boote and Pickering, 1994) and have been tested and shown to work well (Boote *et al*., 2010).

8.4. Pod addition, seed Growth, and partitioning intensity

Increase in temperature, short days, light intensity, high Q and high humidity promote flower numbers in groundnut (Prasad *et al.,* 1999b; Talwar *et al.* 1999; Bagnall and King, 1991a & b and Lee *et al*., 1972). Threshold temperature for pollen production and viability is 34 ^{o}C, above which both pollen production and viability decrease linearly with the increase in temperature (Prasad *et al.,* 1999b). Floral bud temperatures above 36 ^{o}C during AM and whole day significantly reduce fruit-set (Prasad *et al.,* 2000a). Elevated CO_2 does not affect pollen viability (Prasad *et al*., 2003). Peg formation is not affected up to the air temperature range of 33/28 to 35/30 ^{o}C (30.5 to 32.5 ^{o}C), but the pod and seed numbers are decreased. Optimum air temperature for podding is around 36/26 ^{o}C (31 ^{o}C) (Prasad *et al*., 2003). Optimum air temperature for pod growth as suggested by many researchers appears to lie between 20-24 ^{o}C, whereas optimum soil temperature for pod formation and development is between 29 and 33 ^{o}C (Dreyer *et al.,* 1981; Ono, 1979; Ono *et al.,* 1974 and Golombek and Johansen, 1997). Both air and soil temperatures have additive effect on reproductive growth (Prasad *et al*., 2003). Elevated CO_2 increases pod and seed numbers. Long photoperiod decreases number of flowers, pegs and pods and pod weight. Pod numbers are more sensitive to photoperiod than number of flowers and pegs (Bell *et a*l., 1991; Bagnall and King, 1991 a & b). Soil water deficits prevent peg and pod development (Rao *et al*., 1985). High temperature and water stress decreases HI, except when mild water stress occurs prior to flowering (Craufurd *et al*., 2002 and Rao *et al*., 1985). Long days decrease HI and the temperature x

photoperiod interaction was significant for HI. Enhanced CO_2 increases HI. High temperature decreases shelling percentage. Drought reduces shelling percentage when it occurs during pod-filling period.

The CROPGRO groundnut model (Boote *et al.,* 1998) has a parabolic temperature function for relative rate of flower and pod formation per day that has a base temperature of 15 ^{o}C, with an optimum between 20 to 26.5 ^{o}C, declining to zero addition at 40 ^{o}C. The individual pod and individual seed growth rates function (per shell or per seed) in the model depend on a similar parabolic function, with a base temperature of 6 ^{o}C, with an optimum between 21 to 23.5 ^{o}C, declining to zero growth rate at 41 ^{o}C (this is strongly supported by Cox, 1979). In addition, there is a function that reduces partitioning to pods and seeds as maximum temperature exceeds 33 ^{o}C, going to a 0.40 relative value at 46 ^{o}C (but of course, no flowers or pods would be added above 40 ^{o}C). These three functions were found by Boote *et al*. (2010, see their Figure 4) to mimic well the data of Prasad *et al.* (2003), showing that optimum pod yield was at 24 ^{o}C and progressively declined to zero yield at a mean temperature of 39 to 40 ^{o}C. The model also well reproduced data of Cox (1979) showing optimum temperature for pod and seed growth to be about 24 ^{o}C. With coding, these functions could be replaced by explicit temperature effects on transitions from individual flowers to successful pegs and pods using information similar to Prasad *et al.* (1999). The CROPGRO model does allow mild photoperiod effects on seed growth rate of soybean based on reliable data, but data for same effect on groundnut are too tenuous to turn this effect on at present.

8.5. Climatic effects on root growth

The change in root growth or root to shoot ratio at high temperature depends upon the timing, duration and intensity of temperature stress in relation to crop growth stage. Optimum temperature for root growth is close to 30 ^{o}C (Suzuki, 1966). Generally, both high air and soil temperatures above 30 ^{o}C decrease dry matter partitioning to roots. Soil water deficit and enhanced CO_2 increase root growth. High temperature and enhanced CO_2 decrease root to shoot ratio, while water stress increases root to shoot ratio.

The effects of CO_2 and water stress on root growth are indirectly taken care of in the model via their effect on plant water deficit and partitioning to roots. Presently, the CROPGRO-Groundnut model does mimic increased root growth under CO_2 enrichment, as well as enhanced partitioning to root as a function of water deficit. However, the direct effects of high temperature on root to shoot ratio are not modeled, unless that operates via enhanced water deficit.

9. CONCLUDING COMMENTS

Groundnut (*Arachis hypogaea* L.) is one of the major oilseed and food crops of the subtropical and tropical regions of the world. It is grown in different rainfall and temperature regimes on a variety of soils. Depending upon the location on the globe,

climate change may benefit or adversely affect the productivity of this crop. This paper has reviewed the current state of knowledge on effects of climate change factors, such as extremes of air and soil temperatures, relative humidity, water availability and their interactions with photoperiod, light intensity and increased atmospheric CO_2 concentration, on the growth and development of groundnut. The review identified research gaps and needs to generate information to upgrade the CROPGRO-Groundnut model. The review revealed that the direct and indirect effects of most climate change factors on plant growth and development processes are well understood and already incorporated in the model. Extreme events associated with climate change such as water-logging, extreme soil water deficiency or extreme humidity conditions will affect the productivity of the crop. Low light intensity affects flowering and high air and soil temperatures affect root growth and root to shoot ratio. The effects of these factors on groundnut crop growth and development need to be sufficiently understood before these are suitably incorporated in the model to enhance its capability for better assessment of climate change impacts and to develop adaptation strategies to cope up with climate change in different agro-climates. Direct comparison of model simulations against experimental data reported in some studies listed in this review, would be useful.

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