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QUANTIFYING THE EFFECTS OF HIGH TEMPERATURE AND WATER STRESS IN GROUNDNUT (*Arachis hypogaea* L.)

By

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To my first teachers - parents
And
To my second parents - teachers

ABSTRACT

Groundnuts cultivated in the semi-arid tropics are often exposed to water stress (mid-season and end-season) and high temperature (>34°C) during the critical stages of flowering and pod development. Research reported in this thesis from controlled environment and field experiments show that both water stress and high temperature reduce pod yields. Water stress reduced pod yield by decreasing both source and sink size, while high temperature reduced pod yield by hampering fertilisation and partitioning. The effects of stress and high temperature were additive and temporary for both vegetative and pod yield, and disappeared as soon as high temperature stress was removed. Genotypic differences for tolerance to high temperature under both controlled environment and field experiments can be attributed to differences in flowering pattern, flower number, peg-set and harvest index. High temperature reduces peg set by reducing pollen germination and pollen tube growth. High temperature tolerance is partly due to the ability of pollen to germinate and grow at extreme temperatures >34°C and this was correlated with base heat tolerance as measured through membrane thermostability. A principle component analysis suggested that genotypes can be screened for tolerance to high temperature based on pollen characters (pollen germination and tube growth). There was no evidence for an improvement in tolerance with prior exposure to acclimation temperatures of 34°C during vegetative and floral bud development stages. The effects of high temperature on vegetative growth and pod yield of groundnut could not be simulated by the widely used simulation model PNUTGRO. The PNUTGRO can be made sensitive to high temperature by incorporating responses to high temperature identified in this thesis and other studies. The identified tolerance can thus be exploited for breeding genotypes to improve groundnut productivity in SAT regions with extreme climates.

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LIST OF ABBREVIATIONS

%	percent
AM	Ante Meridian (before noon)
°C	degree Celsius
°Cd	thermal time in Centigrade days
cv/cvs	cultivar/cultivars
d	day
df	degrees of freedom
DAA	Days after anthesis
DAS	Days after sowing
DBA	Days before anthesis
e.g.	for example
ed/eds	Editor/Editors
eq.	Equation
FAO	Food and Agricultural Organisation
Fig.	Figure
g	gram
h	hour
ha	hectare
i.e.	that is
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
kg	kilogram
kPa	kilopascal
L	Litre
Ltd.	Limited
m	meter
min	minute
p	probability
PAR	Photosynthetically Active Radiation
PEL	Plant Environment Laboratory
s	second
SAT	Semi-Arid Tropic
SE	Standard Error
SED	Standard Error of Difference
sp., spp.	species
T	Temperature
t	ton
T_b	Base Temperature
T_{min}	Minimum temperature
T_{opt}	Optimum temperature
T_{max}	Maximum temperature
UK	United Kingdom
USA	United States of America

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Groundnut (*Arachis hypogaea*, L.) has spread from its centre of origin in the Matto Grosso State of Brazil to most tropical, sub-tropical, and warm temperate regions between 40° North and South latitudes. This dissemination indicates adaptability of groundnut to a wide range of soil and climatic conditions, and to the value of the crop for food, oil, and feed (Cummins, 1986). Estimates of world groundnut production are 23.84 Mt from an area of 34.52 Mha (FAO, 2000), i.e. an average yield of 1448 kg ha^{-1}. Approximately 70% of this production comes from the semi-arid regions and the developing countries contribute about 90% to the total (FAO, 2000). The semi-arid tropics (SAT) in India, Senegal, Nigeria, Sudan, Zaire, Brazil, Burma, Argentina, Thailand and Zimbabwe (Plate 1.1) are characterised by extremes of moisture availability and temperature during the peak period of rainfed groundnut crop cultivation.

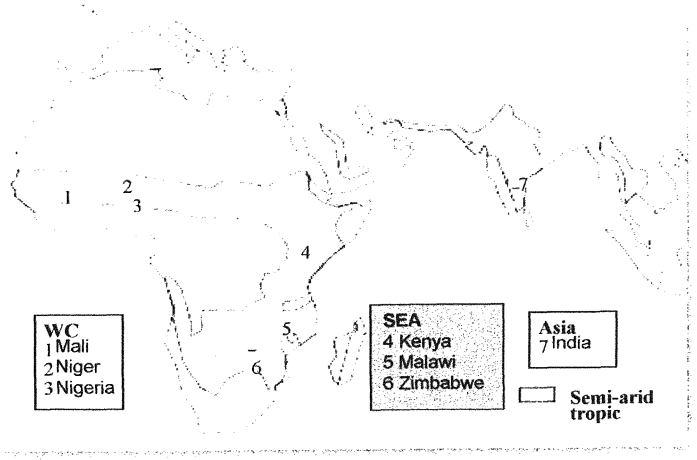


Plate 1.1 The semi-arid tropics of Asia and Africa (WC = western and central Africa; SEA = southern and eastern Africa (Source: http://www.cgiar.org/icrisat/)

Evidence is accumulating for anthropogenic global warming (IPCC, 2000). Observations show that the world has warmed by 0.5 ^{0}C since the late nineteenth century (Kaiser and Drennen, 1993). General Circulation Models (GCMs) indicate a warming of 1.8 to 5.7 ^{0}C for a doubling of CO_2 (IPCC, 2000). Temperature and C concentration are likely to increase at a rate of 0.3 ^{0}C and 2.3 GtC per decade, respectively. The real concern is what might happen if concentrations of key greenhouse gases go on increasing? Venus is the extreme example, with 90% CO_2 in the atmosphere and a surface temperature of 477 ^{0}C !

Global warming has not been uniform regionally nor equal throughout the seasons. Recent analyses of maximum and minimum temperature trends indicate that from 1950 to 1990 minimum temperature over some land areas has risen at three times the rate of change in maximum temperature (Rosenzweig and Parry, 1993). The consequent reduction in diurnal temperature range is approximately equal to the temperature increase. It has been recorded by many scientists that changes in temperature effect vegetative and reproductive growth (Ong, 1986; Ketring, 1984; Wheeler *et al.*, 1997); flowering pattern (Craufurd *et al.*, 2000); basic physiological processes like photosynthesis and respiration (Bhagsari, 1974; Bagnall *et al.*, 1988); and fruit-set (Vara Prasad *et al.*, 1998, 1999a, 1999b, 2000a) in groundnut.

Extensive research has been carried out in groundnuts concerning the effects of water stress (e.g. Williams *et al.*, 1986; Nageswara Rao *et al.*, 1988) but to a much lesser extent on the effects of extreme high temperatures. Various methods have been devised to screen groundnut genotype responses to water

stress, but not so for responses to temperature. Temperature variability can have severe consequences for both individual farmers and on whole regions of production. Temperature tolerance together with appropriate water stress tolerance can deliver better cultivars to a given production area.

Current understanding of global climate change suggests that hot temperature episodes may become more frequent and/or extreme in the future. Given the cultivation of groundnut in the SAT and, as well, the likelihood of global warming, there is an urgent need to understand how to sustain the production of groundnuts because 70% of the world crop is produced in environments where hot temperature episodes may constrain yield (FAO, 2000).

Crop models provide the means to predict biological and economic yield and production risks for a diverse range of environments. Models of crop growth can simulate the effect of different climates, soils and cultural practices more cheaply than by doing all of the work in the field. Models can be used to examine the potential of climates predicted by the GCMs for future years. They can also examine the effects of extreme temperature events, either by increasing the variability of current climates, or by running many hundreds of climate years and looking at the extremes. Models can draw attention to gaps in understanding and thereby stimulate new experimental work or theoretical scenarios. Crop models can be useful for analysing experimental results by virtue of their ability to substantiate possible causes of difference in the results of statistical analysis, and so provide a level of interpretation beyond the bounds of statistical

significance that currently guide the analysis of crop experiments (Sinclair and Seligman, 1996).

Groundnut growth, development and yield have been simulated by simulation models such as: PEANUTGRO (Boote *et al.*, 1986); PEANUT (Young *et al.*, 1979); PEANUTZ (Duncan *et al.*, 1978); QNUT (Hammer *et al.,* 1995). The popular model PNUTGRO, had been evaluated and validated for responses to water availability (water stress), sowing dates and seasons, plant population and row spacing. PNUTGRO has not been evaluated or validated for response to high temperature stress or for the effects of interaction between water stress and high temperature on groundnut growth, development and yield.

These gaps in understanding of response to water stress and high temperature were the subject of the research presented in this thesis. A brief review in Chapter 2 describes the current knowledge on water stress and high temperature effects along with the current state of crop modelling. The interaction between water stress and high temperature is presented in Chapter 3 (controlled environment) and Chapter 6 (field conditions). Genotypic differences for pollen and membrane thermostability to high temperature are presented in Chapter 4. Evidence for acclimation response in groundnut genotypes is presented in Chapter 5. In Chapter 7, the PNUTGRO model is validated with the results from Chapter 3 and 6. Finally, in Chapter 8 a general discussion of the observed results, with an insight into future research for high temperature tolerance in groundnuts is presented.

CHAPTER 2

REVIEW OF LITERATURE

2.1 INTRODUCTION

Plants are able to control the temperature of tissue through transpiration, which can cool leaves by as much as 6-7°C relative to ambient air (Fisher, 1980). High temperatures may cause problems (e.g. necrotic lesions, chlorotic mottling, denaturation and aggregation of proteins) if water is not readily available. Thus, water stress results in an increase in plant temperature (Sanders *et al.*, 1985a). In Rajasthan State of India, for example, air temperatures during the growing season often exceed 40°C, and soil temperatures of more than 60°C are frequent during the middle of the day. The occurrence of high temperature combined with water stress is common in the SAT (Nix, 1975).

The groundnut growing regions within the SAT are typically subject to extremely high temperatures (35° to 45°C), which constrain growth and yield. An increase in the availability of irrigation facilities is also spreading the cultivation of groundnuts to areas with extreme climatic conditions (FAO, 2000). Temperature is the dominant factor controlling the rate at which groundnuts develop (Fortanier, 1957; De Beer, 1963; Cox, 1979). Studies have indicated that the flowering period is particularly sensitive to the effects of high temperature (De Beer, 1963). Increases in soil temperature (>28°C) along with high air temperature (>34°C) are also an important constraint to pod formation and development (Vara Prasad *et al.*, 2000b).

In addition to extreme climatic conditions, farmers in the SAT also face economic constraints due to low income per unit of cultivated area and large family size. To avoid overburdening of already constrained systems with poverty

alleviation, low cost crop-testing systems are required. Crop models offer a suitable surrogate to simulate crop growth and development under these climatic and economic conditions, thus helping to target research in the SAT areas more effectively.

The objective of this review is to explore how temperature affects the growth and development of groundnut. Temperature effects on flowering, including flower production and the formation of the ovary and pollen, are discussed in detail. The literature on acclimation to temperature in plants is also briefly reviewed. Temperature extremes and water stress often occur together and the effects of any interaction between these two stresses are complex and poorly understood. The impacts of these limitations are also reviewed here. Finally, crop simulation models that are purported to simulate responses to high temperature and water stress in groundnut are discussed.

2.2 PHYSIOLOGY OF TEMPERATURE EFFECTS IN GROUNDNUT

2.2.1 Temperature effects on development

Development in plants has been defined as a sequence of phenological events controlled by environment (Landsberg, 1977). In groundnut as in other annuals, temperature moderation of development can be expressed in terms of thermal time above an appropriate base value (Angus *et al.*, 1981; Ketring and Wheless, 1986; Nigam *et al.*, 1994) or days after sowing or absolute temperature (Fortanier, 1957; Leong and Ong, 1983; Talwar *et al.*, 1999). A detailed account of the temperature effects on groundnut growth and development has been provided by Ong (1986). The research reviewed here concentrates on absolute temperature effects on developmental events in groundnut.

2.2.1.1 Germination

The time from sowing to seedling emergence (d) as well as the proportion (%) of seedlings that emerge are influenced by temperature (Mixon *et al.*, 1969; Angus *et al.*, 1981; Garcia-Huidobro *et al.*, 1982; Leong and Ong, 1983; Ketring and Wheless, 1986; Mohamed *et al.*, 1988a, 1988b; Nigam *et al.*, 1994). The optimum temperature for maximum (%) germination of 15 cultivars of groundnut was in the range of 28° to 36°C (Mohamed *et al.*, 1988a). Temperatures warmer than 36°C were supra-optimal and the critical upper limit to germination is reported to be 54°C (Dickens and Khalsa, 1967).

2.2.1.2 Leaf and node appearance

Leaf number, plant height and main stem node number in groundnut are all responsive to temperature. An increase in leaf number occurs with increase in

temperature (Fortanier, 1957; Garcia-Huidobro *et al.*, 1982; Talwar *et al.*, 1999) and this response varies with genotypes (Ketring, 1984), i.e. some genotypes are more sensitive than others. Leaf number of cv Schwarz 21 increased, from 17 to 86 plant^{-1}, with an increase in day temperature from 15 to 35°C (Fortanier, 1957). In contrast, Ono *et al.* (1974) recorded a decrease in leaf emergence rate from 4 to 2 leaves d^{-1} with cvs Chiba-handachi, Java no. 13 and Chiba no. 43 as air temperature increased from 20° to 30°C.

The rate of node number is accelerated as temperature increases (Fortanier, 1957; Ono *et al.*, 1974; Leong and Ong, 1983; Ketring and Wheless, 1986; Talwar *et al.*, 1999). The optimum temperature for a node to appear in cv Robut 33-1 was 27°C (Leong and Ong, 1983). Increase in node number was recorded up to an optimum value of 35°C by Fortanier (1957). Similarly, increase in branch number due to increase in temperature was recorded by Ono *et al.* (1974) and Talwar *et al.* (1999).

Increase in branch number as well as internode elongation gives rise to longer stems. Day temperature increases from 15° to 30°C increased stem length from 0.2 to 1.6 m, under a constant night temperature of 20°C (Fortanier, 1957). Any further increase in day temperature resulted in a smaller increase in stem length. Increase in air temperature also increases soil temperature and Golembek and Johansen (1997) recorded more leaves and longer stem in cvs TMV 2, AH 6197 and Comet, with an increase in soil temperature from 20°/14°C to 38°/32°C (day/night).

2.2.1.3 Leaf Area Index

Temperature can influence carbon assimilation by the crop canopy by affecting the initiation, expansion, senescence, longevity and death of leaves and therefore canopy leaf area at any one time. An increase in leaf area with increasing temperature can result from an increase in the rate of leaf initiation (Fortanier, 1957) or an increase in individual leaf area or both (Wood, 1968). Several researchers have reported the maximum leaf area of groundnut at a temperature of close to 30°C (Williams *et al.*, 1975a, Cox, 1979, Talwar *et al.*, 1999). Leaf area increases were closely paralleled to increases in dry weight over temperatures of 15°/10°C to 33°/28°C. In Zimbabwe, Williams *et al.* (1975b) recorded a maximum leaf area index (LAI) of 7.0 at 23°C mean temperature, whereas LAI declined to 3.0 at 18°C.

Relatively very small values of leaf area can result from reduced individual leaf size or smaller leaf emergence rates. In contrast to the above observations, increase in day temperature from 30° to 35°C were supra-optimum and reduced average area per leaf cv Tamnut from 4000 to 2500 mm^2 (Ketring, 1984), thus reducing total leaf area.

2.2.1.4 Time to first flower

Initiation of flowers and subsequent flower production (i.e. flower number per plant) play a vital role in the reproductive cycle as they determine the potential sink size and the duration of seed filling. However, actual sink size is often limited by environmental stresses. Variations in the duration from sowing to flower opening in groundnut are correlated to mean temperature (Fortanier,

1957) and thermal time (Wood, 1968; Leong and Ong, 1983; Ketring and Wheless, 1986; Flohr *et al.*, 1990).

As for germination and leaf production, genotypes also differ in their time to flowering in response to temperature. At 24°/19°C time to flowering took 19 d longer for Spanish types, 16 d longer for Virginias and 18 d longer for Valencia's than in similar plant types grown at 30°/25°C (Bagnall and King, 1991a). Warmer temperatures hasten flower initiation (Bell *et al.*, 1991b; Talwar *et al.*, 1999; Ishag, 2000). In the experiments of Bagnall and King (1991b), the rate of progress from sowing to first flower (d^{-1}) showed a positive linear relation with temperature over the range 21° to 30°C. Plants grown at 33°/23°C (day/night) temperatures flowered 2-3 d earlier than those at 33°/17°C (Bell *et al.*, 1991b).

2.2.1.5 Time to peg and pod initiation

Once fertilisation is complete, the fertilized ovary (gynophore) begins to elongate geotropically towards the soil within 5-7 d after flowers are fertilized (Smith, 1950). An intercalary meristem, which is most active in the region 1.5 to 3.0 mm below the base of the ovarian cavity, is responsible for the rapid growth of the peg during the aerial and early subterranean phases of fruit development (Jacobs, 1947).

Peg initiation rate increases as temperature increases from 19°-23°C (Williams *et al.*, 1975b). In terms of thermal time, Flohr *et al.* (1990) calculated that peg initiation occurs when the plants have accumulated 660°Cd above a base temperature of 10°C. The optimum air temperature for pod development, is

about 25°C (Wood, 1968; Cox, 1979) that varies with the cultivar used. Bohlius and DeGroot, as early as 1959, identified that optimum temperature for pod development in the varieties they studied to be between 26° and 28°C. The response of these various developmental events to temperature are presented in Fig. 2.1 and summarised in Table 2.1.

Table 2.1 Values of base temperature (T_b) and thermal time (°Cd > T_b) of several developmental processes of groundnut cv Robut 33-1. (Source: Ong, 1986).

Development process	T_b (°C)	Thermal time (°Cd > T_b)
Leaf production	10.0	56 leaf^{-1}
Branching	9.5	103 branch^{-1}
Time from sowing to first flowering	10.8	538
Time from sowing to first pegging	10.6	670
Time from sowing to first podding	11.4	720

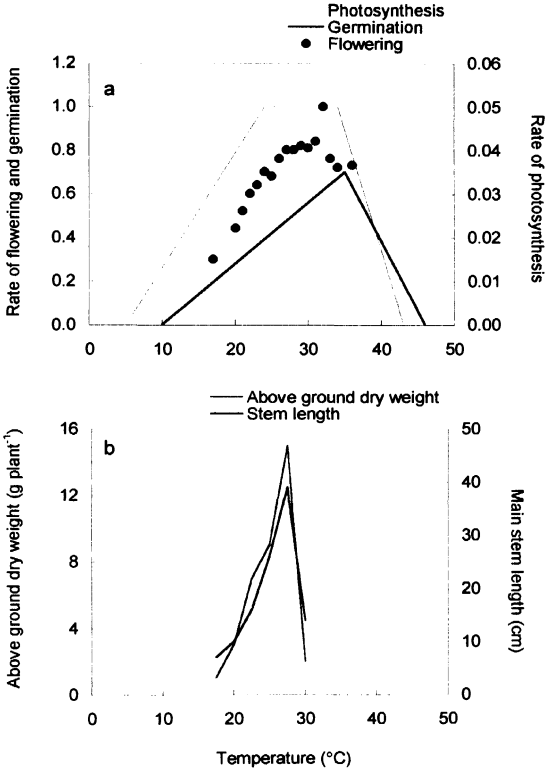


Fig. 2.1 Effect of mean temperature on (a) rate of germination, flowering and photosynthesis; (b) main stem length and above ground dry weight. (Source: Fortanier, 1957; Boote *et al.*, 1978; Mohamed, 1984).

2.2.2 Temperature effects on flower, peg and pod number, and dry matter accumulation

Developmental modifications by temperature accompanied by direct temperature effects on growth processes combine to influence dry matter accumulation and its partitioning to economic yield.

2.2.2.1 Flower number

Flower production in groundnut is affected by temperature (Fortanier, 1957) and the effects have been quantified recently by Vara Prasad *et al.* (1999a). Flower number was reduced at the rate of 1.1 plant $^{-1}$ °C^{-1} between a day temperature of 28°C and 48°C and the ceiling temperature at which no flowers were produced was 54.5°C (Vara Prasad *et al.*, 1999a). A decrease in flower number was also recorded at 80 DAS with increase in day (20° to 35°C) or night temperature (23° to 32°C) (Fortanier, 1957).

Similar negative effects on flower number by high temperature have been recorded in different crops. For example, on exposure to high temperature (39°/28°C day/night), a 17% reduction in flower number was recorded in tomato (*Lycopersicon esculentum* L.) cultivars (Peet *et al.*, 1997). In contrast Kigel *et al.* (1991) reported prolific flower production (135 plant^{-1}) in cowpea (*Vigna unguiculata* L.) when exposed to high temperatures of 32°/27°C (day/night), compared to 52 flowers per plant exposed to 27°/17°C temperature.

Reduction in flower number can also occur if flowers drop due to abscission when plants are exposed to severe or stressful environments. Groundnut flowers wither by midday (Pattee and Mohapatra, 1986). Studies have not been conducted to see if withering is hastened by high temperatures. However, physical flower drop not reported in groundnut, is of general occurrence in many crop plants when exposed to supra-optimal temperatures. A flower bud drop of 66% was recorded in the heat-sensitive tomato cv Hosen-Eilon, whereas only 10% flower drop was recorded in the tolerant cv Hotset at the same temperatures (Levy *et al.*, 1978). Similar differences for flower and bud drop were also observed in bean (*Phaseolus vulgaris* L.) genotypes when exposed to temperatures of ≥ 35°C (Monterrosso and Wein, 1990).

2.2.2.2 Peg and pod number

In controlled environment studies, peg number was affected by both high day and high night temperatures (Vara Prasad *et al.*, 1999a, 2000a). Increase in day temperature from 28° to 48°C reduced peg number at the rate of 0.9 plant^{-1} °C^{-1}. Increase in night temperatures reduced peg number from 7.7 to 5.0 plant^{-1}. In contrast, no such decrease in peg number was recorded by Dreyer *et al.* (1981) in their study with soil temperatures of 23°, 27°, 30°, 34° and 37°C.

Decreases in flower and peg numbers reduce the number of pods formed. In a study by Vara Prasad *et al.* (2000b), pod number was decreased by high air temperature (38°/22°C) and by high soil temperature (38°/30°C). High air temperature at podding reduced pod number by 32% whilst high temperature at flowering reduced pod number by only 22%. However, high soil temperature had

the opposite effect. High soil temperature at flowering reduced pod number by 52% while at podding the loss was only 33%. Thus a combination of these extreme air and soil temperatures, which are common in the SAT (Nix, 1975), will greatly reduce pod numbers and yields.

2.2.2.3 Dry matter accumulation

The amount of dry matter accumulated in groundnut per unit input (light, water and nutrients) determines the overall efficiency of the production system. Crop growth rate, which indicates the rate of conversion of inputs into dry matter, is influenced by temperature.

Temperatures above or below an optimum value reduce dry weight or biomass accumulation. An optimum temperature of 30°/26°C has been identified for dry matter accumulation. Temperature 4°C above or below the optimum of 28°C, reduced dry weight (Cox, 1979). Temperatures > 38°C during the day reduced dry matter production (Wood, 1968; Wheeler *et al.*, 1997; Craufurd *et al.*, 1999; Vara Prasad *et al.*, 1999a) and decreases in biomass by 25% at 35°C (Wood, 1968) to 50% at 45°C (Wheeler *et al.*, 1997) has been recorded compared to that at 25°C.

Soil temperature is also important in determining groundnut yield as the pod growth occurs in the ground. Vara Prasad *et al.* (2000a) reported a decrease in per plant dry weight with increase in air or soil temperature. High air (30°/25°C) or high soil (25°/34°C) or high air combined with high soil (30°/34°C) temperatures reduced dry weight plant^{-1} by 20, 50 and 55%, respectively. An

increase in soil temperature alone also affects dry matter accumulation: an increase from 20°/14°C (day/night) to 32°/26°C, decreased the dry matter accumulation of stems, leaves and roots (Golembek and Johansen, 1997).

2.2.2.4 Partitioning to pod and pod growth

Pod yield is usually correlated positively with total dry matter accumulation (Uguru, 1998) and therefore any effect of temperature on total dry matter accumulation will effect pod yield (Ono *et al.*, 1974; Cox, 1979).

Once the peg penetrates the soil, the growth of the peg and that of the pod is influenced more by soil temperature than by air temperature. Maximum yield and quality will be produced when the geocarposphere temperature is between 21° and 29°C during pod addition and pod maturation periods (Davidson *et al.*, 1991).

A decrease in fruit yield per unit area was recorded due to a decrease in the duration of the pod filling period under high soil temperature conditions. Dreyer *et al.* (1981) observed that at soil temperatures of 30° to 34°C pods have greater growth rates than at 23°C. Although higher pod growth rates were observed at high soil temperatures (32°C), a decrease in pod yield occurred due to decrease in pod initiation rate (Golombek and Johansen, 1997).

Combinations of high air and soil temperatures are especially detrimental to pod yields. Vara Prasad *et al.* (2000b) reported that when high air and high soil temperature were experienced during the flowering and podding periods, pod

yields declined largely in an additive manner: by 18-26% at high air temperature, 30-39% at high soil temperature, and 49-52% by a combination of high air and soil temperatures.

Studies on the effects of temperature on biomass partitioning in groundnut are inconclusive. Partitioning has been identified as the main cause for yield reductions in controlled environments (Wheeler *et al.*, 1997) and in the field studies (Ntare *et al.*, 1998). Ntare *et al.* (1998) showed that decline in partitioning is more closely related to minimum temperature than to maximum temperature during the day because the minimum temperature occurs during the periods of fertilisation in groundnut. In a recently reported study by Ntare *et al.* (2001) higher pod yield was significantly associated with greater partitioning to pods (Fig. 2.2), hence genotypes (e.g. 55-437, ICG 1236) which fall in Group 1 were considered tolerant. In studies by Wheeler *et al.* (1997) a day temperature of 45°C reduced HI to 87% and 41% of the value in the control (30°C) plants in high temperature-tolerant (HTT) and high temperature-sensitive (HTS) genotypes, respectively. In contrast, in a study with two Virginia and two Spanish cultivars in Australia, Bell *et al.* (1991a, 1993) recorded an increase in partitioning with increase in night temperature, from 17° to 23°C, at a constant high temperature during day (33°C). These studies indicate that differences for partitioning at high temperature exist in groundnut genotypes.

2.2.2.5 Root growth

Roots growth compensates for the effects of above ground stress events, like high temperature, by supplying additional water and nutrients to the shoot under

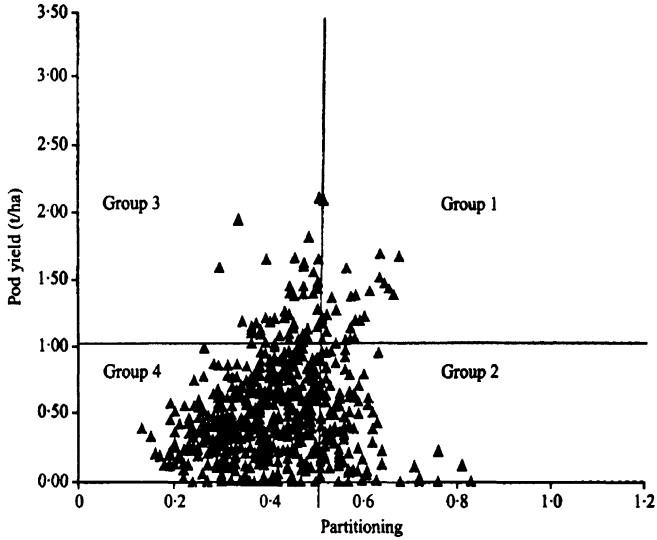


Fig. 2.2 Classification of 625 groundnut genotypes based on pod yield (t ha^{-1}) and partitioning (proportion of dry matter partitioned into reproductive sinks) in 1991. (Source: Ntare *et al.*, 2001).

stress. Any injury to the roots due to the high air temperature may aggravate the stress effects. In the Spanish cv Spantex, root dry weight decreased rapidly with increasing temperature so that root weight at 35°C was only 35% of that recorded at 20°C after 47 d from sowing (Wood, 1968). There was no effect of night temperature *per se* on root growth.

In a study comparing the performance of HTT and HTS genotypes, Wheeler *et al.* (1997) recorded that root biomass declined in both genotypes at 45°C. The decline in the root biomass of the HTS genotype ICGV-SM-86021 was more rapid, than in the HTT genotype 55-437 during the 41d period after flowering. Thus, high temperatures advanced the natural ontogenic decline in root-shoot ratio which occurs as groundnut crops progress through the reproductive phase to maturity and death (Wheeler *et al.*, 1997).

The effects of soil temperature on root growth are less well understood. For example, high soil temperature between flowering and maturity increased the amount of dry matter partitioned to roots in the study of Vara Prasad *et al.* (2000b). In contrast, Golombek and Johansen (1997) observed a decrease in root weight with increase in soil temperature from 20°/14°C (day/night) to 38°/32°C, when imposed from emergence to maturity. Hence, further studies are required to find the critical temperature, growth stage, and genotypic differences for root growth.

2.2.3 Temperature effects on pollen, stigma and ovary

Pollen grains once dispersed from the anther remain as independent functional units and are exposed to the prevailing environmental conditions for various periods. Depending on the period and severity of the environment, the quality of pollen grains, particularly their viability and vigour, may be affected during this pre-pollination phase (Shivanna and Sawhney, 1997).

Extensive work has been undertaken in several legumes and cereals on the processes of pollen production, pollen germination and pollen tube growth when exposed to high temperatures. These studies have established beyond doubt that high temperatures reduce pollen viability, pollen germination, and pollen tube growth (Farlow *et al.*, 1979; Herrero and Johnson, 1980; Saini and Aspinal, 1982; Saini and Westgate, 2000).

High temperatures are also known to reduce progress in ovary and embryo development (Ahmadi and Stevens, 1979; Saini *et al.*, 1983). It has also been established that genotypic differences exist for pollen tolerance to high temperature. The following review summarises the effects of temperature on pollen, stigma and ovary. Stages in the life of a groundnut flower and with special reference to pollen are presented in Plate 2.1.

2.2.3.1 Pollen Viability

Not much is understood about high temperature effects on groundnut pollen which is tricolpate and bicelled with a large vegetative nucleus and a small generative nucleus (Xi, 1991). In a recent study, Vara Prasad *et al.* (1999a)

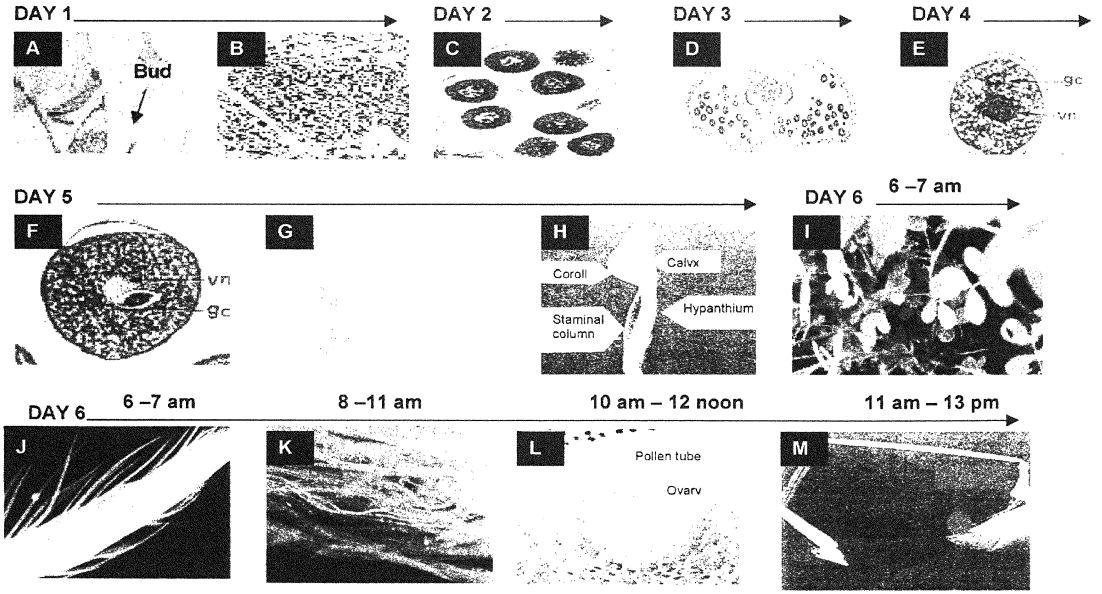


Plate 2.1 Stages in the 6 d life of a groundnut flower with special reference to pollen. Day 1: bud initiation occurs (a), sporogenous tissue in anther (b); Day 2: tetrad stage of dividing pollen mother cell (c); Day 3: separated very early microspores in anther lobes (d); Day 4: Young pollen grain dividing into generative (gc) and vegetative (vc) cells (e); Day 5: Mature two celled pollen grain (f, g), hypanthium elongation (h); Day 6: Anthesis (i), pollination (j), pollen tube growth in style (k), fertilisation – pollen tube (pt) in ovule (l), withered flower (m). (Source: Xi, 1991; Pattee and Mohapatra, 1986).

reported that groundnut pollen viability as assessed by staining with 2,3,5, triphenyle tetrazolium chloride (TTC) was reduced when pollen was exposed to night temperatures of 22° and 28°C with day temperatures increasing from 28° to 48°C (Fig. 2.3). A threshold temperature of 34°C was recorded for pollen viability, and there was a strong linear negative relation between fruit set and pollen viability at temperatures > 34°C. Further studies are needed to confirm the role of pollen viability in peg and pod set in explaining genotypic differences in response to high temperature.

Pollen viability of other crop plants has been studied using various staining techniques. Staining tests with TTC (Weaver *et al.*, 1985), Alexanders stain (Shelby *et al.*, 1978), propionic caramine (Halterlien *et al.*, 1980), flurochromatic reaction (Baki, 1992), were used to study pollen viability in different crop species. Along with staining techniques, cross pollination (Dickson and Boettger, 1984; Gross and Kigel, 1994) and pollen germination tests (Rudich *et al.*, 1977) have also been used in crops to indicate the viability of pollen exposed to different temperature regimes.

In a study by Halterlien *et al.* (1980) with four cvs of bean (PI 271997, Oregon 1604, UI 111 and Bontac), no differences were found in the viability of pollen at the lowest temperature, 25°/20°C. However, at high temperature (35°/20°C) the pollen viability of PI 271997, for example, was reduced, from 86 to 25%. Weaver *et al.* (1985) also reported that pollen viability in newly opened flowers of the high temperature-sensitive bean cv 5BP-7, was reduced by nearly 50% at 35°C and pollen was killed at 41°C. They also noted a significant decrease in viability of

other cultivars. Similar observations were made by Dickson and Boettger (1984), and by Gross and Kigel (1994) in other cultivars.

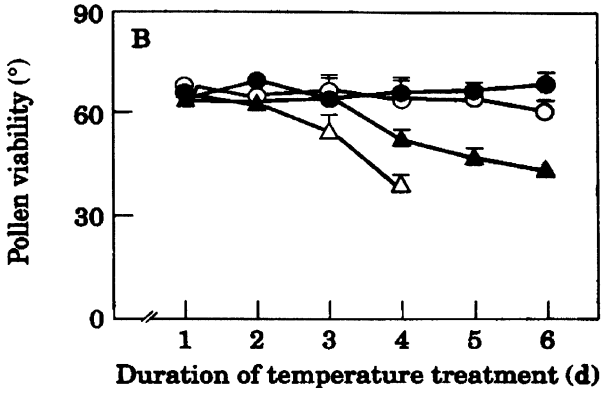


Fig. 2.3 Effect of day temperatures of 28° (•), 34° (○), 42° (▲) and 48°C (Δ) on pollen viability (angular transformed) over time during 6 d period of stress. Bars denote s.e. and are shown where they exceed the size of the symbol. (Source: Vara Prasad *et al.*, 1999b).

Temperature effects on tomato pollen are well documented (Rudich *et al.*, 1977; Shelby *et al.*, 1978; Ahmadi and Stevens, 1979; Weaver and Timm, 1989; Dane *et al.*, 1991). While screening tomatoes for high temperature tolerance, Weaver and Timm (1989) showed that pollen viability was greatly reduced when flowers were exposed to temperatures of 40° and 48°C and genotypes varied significantly in their percent viable pollen. Pollen viability of most tomato cultivars, except for Redcherry and PI 190256, was severely reduced when exposed to temperatures of 35°-36°C (Dane *et al.*, 1991).

Pollen viability has also been studied in maize (*Zea mays* L.) by Schoper *et al.* (1986); Lyakh *et al.* (1991) and in wheat (*Triticum aestivum* L.) by Saini and Aspinall (1982); Zeng *et al.* (1985). In contrast to these studies *Brassica juncea* (L.) Czern. pollen grains remained viable even at temperatures of 60°C, and at 75°C pollen viability was reduced by only 20% (Rao *et al.*, 1992).

2.2.3.2 Pollen germination

Even though pollen grains are viable based on a chemical stain reaction, the ability to germinate and sustain pollen tube growth on exposure to abiotic stress and so the effective fertilisation of the ovary are thought to be more important and not necessarily correlated with percentage viability (Ahmadi and Stevens, 1979). Hence, it is necessary to understand the response of pollen germination to temperature. In the studies reviewed below, a pollen grain is considered to have germinated when the pollen tube is equal to or longer than the diameter of pollen grain under study. The percentage pollen germination and cardinal temperatures for pollen germination in different crop species are shown in Table 2.2.

The Tmin, Topt and Tmax temperatures for groundnut pollen germination in cv Spantex were reported to be 18°, 32° and 35°C, respectively (Oakes, 1958). Not only do crop species differ in their response to temperature, but genotypic differences are also found within-species. In most crops, the maximum/lethal temperature (Tmax) for pollen germination is > 35°C. For example, in tomatoes, pollen germination was severely reduced when temperatures were more than 40°C (Maisonneuve and Den Nijs, 1984; Weaver and Timm, 1989). Weaver and

Table 2.2 Pollen germination (%) at three cardinal temperatures in different crop species.

Crop	Pollen germination (%) at			Temperature (°C)			Reference
	T_{min}	T_{opt}	T_{max}	T_{min}	T_{opt}	T_{max}	
Groundnut (*Arachis hypogaea*)	-	-	-	18	32	35	Oakes (1958)
French bean (*Phaselous vulgaris*)	0.5	85	0.5	4	7	38	Farlow *et al.* (1979)
Snake guard (*Cucumis melo*)	5	100	0	10	37	48	Matlob and Kelly (1973)
Bottle guard (*Lagenaria siceraria*)	-	80	0	-	30	38	Iapichino and Loy (1987)
Chinese cabbage (*Brassica campestris* ssp.*Pekinensis*)	12	41	15	10	20	32	Kuo *et al.* (1981)
Cucumber (*Cucumis sativus*)	10	90	0	10	21	43	Matlob and Kelly (1973)
Muskmelon (*Cucumis melo*)	50	100	-	20	40	-	Maestro and Alvarez (1988)
Pear (*Pyrus communis*)	10	100	-	5	15	-	Vasilakakis and Porlingis (1985)
Avocado (*Persea americana*)	17	65	-	15	25	-	Louppassaki *et al.* (1997)
Walnut (*Juglans* sp.)	6	47	0	14	28	40	Luza *et al.* (1987)

(- = not reported)

Timm (1989) also recorded genotypic differences for pollen response to temperature. Studies are essential in groundnut to identify the genotypic differences for tolerance of pollen to high temperature.

2.2.3.3 Pollen tube growth

Once pollen germinates, it takes between 5 to 6 h in groundnut (Lim and Gumpil, 1984) and 3-4 d in tree species such as apple (Jefferies and Brian, 1984) for the pollen tube to reach the ovary. During this period of growth along the style to the ovary, the pollen tube may be exposed to temperature extremes that increase in severity as the day progresses. Hence, tolerance of pollen tube growth to surrounding environmental extremes may be essential for successful seed set. Differences exist for *in-vitro* pollen tube length among crop species, which can be related to differences in style length. Crops also differ in their cardinal temperatures to pollen tube growth indicating their adaptation to specific conditions (Table 2.3).

Only one record for groundnut pollen tube response to temperature has been published (Oakes, 1958). At an optimum temperature of 32°C, a pollen tube length of 1800 μm was observed in *in-vitro* studies. No pollen tube growth was observed beyond 35°C. Genotypes also differ in their pollen tube growth response to temperature. In tomato cv Grivorski, no reduction in pollen tube length was observed after exposure to 40°C for 60 min. Pollen tube length was reduced by 14% and 21%, respectively, in cvs Patio and VF-6 at 40°C. In other cultivars the reduction was as much as 54% (Weaver and Timm, 1989).

Table 2.3 Final pollen tube lengths (μm) at three cardinal temperatures in different crop species.

Crop	Pollen tube length (μm) at			Temperature (°C)			Reference
	T_{min}	T_{opt}	T_{max}	T_{min}	T_{opt}	T_{max}	
Groundnut (*Arachis hypogaea*)	500	1800	0	18	32	35	Oakes (1958)
French bean (*Phaselous vulgaris*)	30	400	75	4.5	16.7	38.3	Farlow *et al.* (1979)
Snake melon (*Cucumis melo*)	2	700	0	10	32	48	Matlob and Kelly (1973)
Chinese cabbage (*Brassica campestris* ssp. *Pekinensis*)	26	127	66	10	20	32	Kuo *et al.* (1981)
Cucumber (*Cucumis sativus*)	3	270	0	10	21	43	Matlob and Kelly (1973)
Muskmelon (*Cucumis melo*)	48	60	20	20	30	40	Maestro and Alvarez (1988)
Apple (*Malus domestica*)	9190	13490	3780	3.5	18.5	33.5	Jefferies and Brian (1984)
Pear (*Pyrus communis*)	-	-	-	5	25	-	Vasilakakis and Porlingis (1985)
Walnut (*Juglans* sps)	9	61	0	16	33	37	Luza *et al.* (1987)

(- = not reported)

2.2.3.4 Stigma, Style and ovule

Although pollen viability, germination and tube length are very sensitive to high temperature, and are usually the major cause of sterility, the female reproductive structures (i.e. style, stigma and ovary) may also be affected by high temperature.

Little attention has been paid until recently to stigma receptivity under high temperatures in groundnut. However, studies by Talwar and Yanagihara (1999) have shown that high temperatures of 35°/30°C, compared to 25°/20°C, increased hypanthium length and caused stigma exertion, hence reducing the chances of successful fertilisation. Therefore, further studies are necessary to identify the causes for lower fruit-set when exposed to high temperature. Studies are also necessary to quantify the role of male and female reproductive structures in imparting tolerance to high temperature.

Reports on the role of female reproductive parts in inducing sterility under high temperatures are available. Gross and Kigel (1994), from their experiments on common bean, concluded that along with lower pollen viability, female performance was impaired in a large number of flowers resulting in lower fruit-set. Reciprocal crosses made in bean (Monterrosso and Wein, 1990) with pollen from plants grown at high temperature or from heat-treated flowers indicated that pollen was more affected by heat stress than female structures.

In tomatoes, sterility under high temperature (>35°C) conditions has been reported to reduced stigma receptivity (Charles and Harris, 1972), denatured

macrospores (Levy *et al.*, 1978; Ahmadi and Stevens, 1979), and increased style length (Rudich *et al.*, 1977). These morphological changes in stigma and style reduce the chances for successful fertilisation.

When emasculated flowers of tomato exposed to high temperature (37°/27°C) were crossed with normal pollen, a significant decrease in fruit set was recorded in all genotypes (Ahmadi and Stevens, 1979). Studies along similar lines to differentiate the response of male and female tomato organs to high temperatures by Peet *et al.* (1997) indicated that viable pollen supply alone is not sufficient for fruit set under high temperatures.

Saini and Aspinall (1982), from experiments on wheat plants exposed to 30°C, suggested that female sterility may also have contributed to a decrease in grain yield. In a further study, Saini *et al.* (1983) reported that one-third of heat stressed ovaries (30°C for 3 d just prior to anthesis) contained abnormal embryos. Abnormalities ranged from the complete absence of an embryo sac accompanied by reduced nucellus development, to small embryo sacs that contained the full complement of cells. They also observed that when fertilised with fertile pollen, heat stressed stigmas had fewer pollen tubes reaching the ovary, which decreases the chances for a successful fertilisation.

2.3 SCREENING FOR HEAT TOLERANCE

Early identification of tolerance to high temperature in screening trials and crossing studies would enable the breeder to cross genotypes in the same season. Several simple tools have been used to define tolerance to temperature stress in crop plants. Techniques like chlorophyll fluorescence (Sipos and Prange, 1986; Moffat *et al.*, 1990) and cellular membrane thermostability (Sullivian, 1972; Martineau *et al.*, 1979) have been in use to identify crop tolerance to high temperature stress.

2.3.1 Chlorophyll fluorescence

In a study with chickpea (*Cicer arietinum* L.), pigeonpea (*Cajanus cajan* L.), groundnut and soyabean (*Glycine max*), Srinivasan *et al.* (1996) identified groundnut as the most heat-tolerant legume crop based on Fv/Fm (variable fluorescence / maximum fluorescence) ratio. The ratio indicates high thylakoid membrane integrity and stable photochemical efficiency of plant cells (Krause and Weiss, 1984).

Groundnut cultivars differed in their tolerance to temperature stress based on fluorescence test. Cultivars ICG 1236, Florunner and Virginia Bunch were tolerant, whereas Chico, ICGS 44 and Shulamit were highly sensitive to extreme temperature (55°C) (Srinivasan *et al.*, 1996). Chauhan and Senboku (1997) have also shown that chlorophyll fluorescence or chlorophyll concentration can be used to identify tolerance in groundnut. Genotypic differences in Fv response to high temperature stress and the positive relation of Fv and its stability to overall yield were also observed in wheat (Moffat *et al.*, 1990).

2.3.2 Membrane thermostability

Cell membrane thermostability is based on the observation that when leaf tissue is injured by exposure to high temperature, cellular membrane permeability is increased and electrolytes escape.

Selection for membrane thermostability may be a means to improve heat tolerance of the groundnut crop (Ketring, 1986). Groundnut genotypes differ in their response to high temperature for cellular membrane stability with the Spanish cv. ICG 1236 being particularly tolerant (Srinivasan *et al.*, 1996). Similar observations for genotypic differences to membrane thermostability were also made by Chauhan and Senboku (1997).

In general, the groundnuts are more tolerant to high temperature compared with many other crops. Srinivasan *et al.* (1996), in a study with four legumes, showed differences in heat killing temperature (temperature which causes 50% injury) and heat killing time (time required to cause 50% injury at a given temperature). Heat killing temperatures in chickpea, pigeonpea, soyabean and groundnut were 44°, 50°, 51° and 54°C, respectively. Heat killing time was much longer in groundnut (2.3 h) than in soyabean (0.85 h), pigeonpea (0.78 h) or chickpea (0.68 h).

Genotypic differences in membrane thermostability for soyabean were also recorded by Martineau *et al.* (1979). Genotypic differences were greatest in newly developed leaf tissues, and genotypic differences were consistent across

sampling dates, indicating that assay can be conducted during any phase of vegetative growth.

Membrane thermostability has been used to identify tolerance to heat stress at the seedling stage of the cowpea crop. In a recent study reported by Ismail and Hall (1999), a genotype with tolerance to high temperature at flowering and pod set (1393-2-1) had higher membrane stability (lower electrolyte leakage) than the susceptible genotypes (e.g. 1393-2-11 and CB5).

2.4 ACCLIMATION FOR HIGH TEMPERATURE

Acclimation refers to the non-heritable modification of characters caused by the exposure of organisms to new climatic conditions, such as warmer, cooler, or drier weather (Kramer, 1980). Henle and Dethlefsen (1978) have defined heat acclimation/acquired thermotolerance/heat hardening as the ability of organisms to tolerate normally lethal high temperatures due to an initial exposure to an elevated but sub-lethal temperature. Alternatively, heat acclimation has been defined as the ability of plants to increase their tolerance to heat following exposure to acclimation temperatures (Li *et al.*, 1991).

Studies conducted to date have shown that a sudden imposition of high temperature, in controlled environments during the sensitive reproductive phase, reduces fruit set and yield in groundnut (Vara Prasad *et al.*, 1998, 1999a, 2000b; Wheeler *et al.*, 1997). However, under natural conditions in the field, temperature changes are more gradual, and acclimation may occur. Heat acclimation can enable plants to reduce heat injury. Levitt (1980) suggested that thermal tolerance of different genotypes should be compared when plants are at the acclimated stage because the ability of genotypes to tolerate high temperature is significantly and differentially affected by their heat acclimation potential. That is the ranking of heat tolerance for a given group of genotypes may vary depending on whether or not the exposure to high temperature was preceded by heat acclimation.

Acclimation of plant processes such as photosynthesis (Berry and Bjorkman, 1980; Bjorkman *et al.*, 1980) and respiration; acclimation of enzymatic activity

(Teeri *et al.*, 1980) and acclimation of membrane activity (Raison *et al.*, 1980) are well documented in the literature for a number of crops, but not for groundnut. In common bean, Chaisompongan *et al.* (1990) expressed photosynthetic acclimation to high temperature in terms of O_2 evolution. Without heat acclimation, heat stress at 42°C decreased O_2 evolution in six genotypes from 50 to more than 95% compared with the control. A 45°C heat stress almost inhibited O_2 evolution. In plants acclimated to heat by placing them at 37°C for 24 h, heat stress at 42°C had no effect on O_2 evolution. However, little is known as to how acclimation of these processes results in increased grain yield of field crops exposed to high temperatures.

Two genotypes each of bean, potato (*Solanum tuberosum* L.), and soyabean and tomato, with known differences in heat sensitivity based on their yield and fruit set under high temperatures, were used in a study of acclimation of leaf tissues to heat stress (Chen *et al.*, 1982). Tomato cv. Saladatte (heat tolerant) and UC-82B (heat susceptible) were both killed after about 15 min at 50°C, when plants were grown in a 20°/15°C day/night temperature regime. However, after a 24 h treatment at 40°/30°C, the heat-killing time of Saladatte was increased to 65 min, while sensitive UC-82B could survive up to 50 min. Similarly in beans, heat killing time for leaf tissue increased from 5 to 85 min in BBL-415-1 (HT) and from 5 to 50 min in BBL-47 (HS). The acclimating temperatures at which genotypes showed difference in heat killing temperature was 37.5°C for soyabean and potato, and 40°C for tomato and bean. Similar studies in common bean by Li *et al.* (1991) support these findings.

Acquired thermotolerance has also been reported for reproductive process such as pollen tube growth. If the incubation temperature of pollen is raised gradually by 4°C increments every 15 min from 29° to 41°C, pollen tube growth continues at 41°C in *Tradescantia paludosa*, although at a rate slightly slower than for the tubes growing at 29°C (Altschuler and Mascarenhas, 1982; Mascarenhas and Altschuler, 1983; Xiao and Mascarenhas, 1985). No growth was observed in pollen exposed directly to 41°C.

Ability of crop plants to acclimate to high temperature is useful only when it is reflected in terms of economic yield. Most acclimation studies have been process-oriented and did not concentrate on relating acclimation to yield. Studies in wheat by Stone and Nicolas (1995) have shown that mechanisms exist in plants that could translate acclimation potential into economic yield. In their study with two wheat cvs Oxley and Ergot, a sudden rise to high temperature (40°C) resulted in a greater reduction of wheat yield (25%) than in response to a gradual (6°C h^{-1}) rise to midday and a later fall (6°C h^{-1}) of temperature resulted in 10% reduction only in the sensitive variety Ergot.

Studies on groundnut acclimation to heat stress are yet to be conducted. Hence, there is a need to conduct research of groundnuts to identify if any acclimation mechanism to heat stress exists, before developing heat tolerant/resistant cultivars.

2.5 PHYSIOLOGY OF WATER STRESS IN GROUNDNUT

Water stress is one of the major environmental factors limiting groundnut yield in the tropics and sub-tropics (Virmani and Singh, 1986). Erratic rainfall is also responsible for yield fluctuations in these areas (Kanwar *et al.*, 1983). The effect of water stress on groundnut growth and development depends on the stage of crop growth, the duration of water stress, and the intensity of the stress. Ninety percent of the variation in yield in a study with 800 genotypes and 12 different water stress patterns, were accounted for by the intensity of water stress, and the cumulative duration of the stress/(es) (Williams *et al.*, 1986). This literature review concentrates on the effects of water stress on growth, development and yield.

2.5.1 Water stress effects on development

Certain stages of crop development are more sensitive to water availability than the others. Groundnut developmental stages close to flowering and the post-flowering stages are especially sensitive to water stress. Hence, the following review concentrates on these stages.

2.5.1.1 Leaf and branch appearance

Water stress inhibits leaf expansion and stem elongation through a reduction of relative turgidity (Slatyer, 1955; Allen *et al.*, 1976; Vivekanandan and Gunasena, 1976), thus altering both leaf and stem morphology.

Water stress imposed during early flowering phase reduced leaf number significantly more than stress at pod development phase as recorded at maturity

(Ike, 1986; Nageswara Rao *et al.*, 1988; Stirling *et al.*, 1989). The intensity of water stress also modifies leaf number by reducing the size and rate of leaf production (Illina, 1958; Lin *et al.*, 1963; Ong *et al.*, 1985).

In a study with cv. Robut 33-1, differences in leaf number were apparent as early as 30 DAS. After 60 DAS total leaf number in 1, 2, 2.5 and 3 kPa water stress treatments was reduced by 11, 28, 38 and 49%, respectively relative to the control (irrigated) treatment (Ong *et al.*, 1985). The rate of leaf production also declined in this study from 0.3 to 0.23 leaves d^{-1} as soil water deficit increased from 10 to 80 mm.

The main stem and coteledonary branches were fewer in number and also shorter in water-stressed groundnut plants (Ochs and Wormer, 1959; Lin *et al.*, 1963; Su *et al.*, 1964; Gorbet and Rhoads, 1975; Boote and Hammond, 1981). In a study by Nageswara Rao *et al.* (1988) water stress (total water use = 550 mm) during flowering reduced internode length to 90 mm whereas it was 170 mm in the irrigated (total water use = 725 mm) treatment. Similarly branch number was also less (9 $plant^{-1}$) in water-stressed plants compared to irrigated plants (15 $plant^{-1}$).

2.5.1.2 Leaf Area Index

Reductions in leaf number and individual leaf size contribute to decreases in leaf area (Ong, 1984; Ong *et al.*, 1985; Kulkarni *et al.*, 1988; Ravindra *et al.*, 1990). The extent of the reduction is determined by the intensity and duration of water

stress and stage of crop at which the stress is imposed (Nageswara Rao *et al.*, 1988; Meisner and Karnok, 1992).

Meisner and Karnok (1992) measured LAI at harvest for water stress imposed at various stages of crop growth. Water stress imposed by withholding irrigation and imposed for a 30 d period beginning at 20, 50, 80, or 110 DAS reduced LAI significantly to between 5.0 and 5.7 when compared with control value of 6.45. Similar observations were made by Kulkarni *et al.* (1988) and Nageswara Rao *et al.* (1988).

2.5.1.3 Time to first flower

Only severe water deficits delay flowering. Illina (1958) reported that flower initiation was delayed when soil moisture was maintained at or dryer than 35% field capacity. In most studies, there was just a 1-2 d delay (Illina, 1958; Lin *et al.*, 1963; Lenka and Misra, 1973). In contrast, pre-flowering water stress had no effect on the time to flowering in a series of water stress treatments studied by Nageswara Rao *et al.* (1988). Similarly, Nautiyal *et al.* (1999) also recorded that all cultivars in their study flowered between 37 and 39 DAS, irrespective of the intensity of water stress imposed during the pre-flowering phase.

2.5.1.4 Time to peg and pod initiation

The culmination of successful fertilisation results in pegs leading to pods. Water stress either reduces or stops sink development based on the degree of stress. Sink initiation ceased in all the cultivars within 9 d of the start of the water stress treatment, but resumed within 4 d of rewatering (Chapman *et al.*, 1993c). The

rate of peg elongation in these water deficit treatments was halted 3-4 d after the initiation of water deficit (Chapman *et al.*, 1993c).

In a study with cv. Kadiri-3, at ICRISAT in India, Stirling and Black (1991) recorded peg initiation at 45 DAS in the rainy season when VPD averaged to 1-2 kPa. However, at the same location peg initiation was observed at 70 DAS in the dry season when VPD was 4-6 kPa. A delay in peg initiation results in a delay of pod initiation. Stirling *et al.* (1989) also recorded that pod initiation occurred at 52 DAS in the rainy season but it was delayed until 110 DAS in the dry season. Similar delays in peg and pod initiation under water stress conditions were made by Rajendrudu and Williams (1987) and Sexton *et al.* (1997)

2.5.2 Water stress effects on growth

2.5.2.1 Flower number

Total flower number decreases when water stress is experienced during the pre- or post-flowering stage (Nageswara Rao *et al.*, 1988; Ravindra *et al.*, 1990; Ferreria *et al.*, 1992; Meisner and Karnok, 1992; Patel and Golakiya, 1993; Nautiyal *et al.*, 1999).

With cv. Florunner (Meisner and Karnok, 1992), water stress imposed by withholding irrigation for a 30 d period at 20, 50, 80 and 110 DAS and was compared with an adequately irrigated treatment. Water stress which began at 20 and 50 DAS reduced flowering. On rewatering, flowering recovered and continued for 10 d longer than in the control treatment. At later stages only a slight decrease in flower number occurred. Rewatering of the late-stressed plants

did not result in any flowering as flowering stopped at 110 DAS. Thus, reduction in flower number is significant if water stress occurs during early period of flowering. Similar observations were reported by Janamatti *et al.* (1986), and Patel and Golakiya (1993).

2.5.2.2 Peg number and growth

Peg number is reduced when water stress is imposed. A decrease in peg number was recorded by Chapman *et al.* (1993a): when water stress was imposed during the peg development period plants produced only 58 pegs plant^{-1}, whereas control plants produced 76 pegs plant^{-1}.

Under water stress conditions pegs may fail to reach the soil due to a decrease in turgidity due to water stress that restricts the rate of peg elongation. Peg production was insensitive to water potential in the range of –0.53 to –0.76 MPa but the rate declined rapidly below –0.82 Mpa (Chapman *et al.*, 1993a). The rate of peg elongation in these water deficit treatments halted 3-4 d after initiation of water deficit. Peg elongation rates were around 0.5 to 0.6 mm d^{-1} in all cultivars whereas water deficit during the early reproductive period (49-84 DAS) reduced the peg elongation rates to 0.1 to 0.2 mm d^{-1}.

Cultivars differ significantly in peg set (percentage flowers forming pegs) under water stress conditions. In a study with cvs J-11 and M-13 in India, 64 and 75% of flowers formed pegs, respectively, in the irrigated treatment. The percentage was reduced to 46 and 67% in these cultivars under unirrigated treatment (Bhatia *et al.*, 1984).

2.5.2.3 Pod number and growth

The proportion of subterranean pegs converted to pods was reduced by drought at all stages of post-flowering growth (Rajendrudu and Williams, 1987) but most severe effect was recorded when water stress occurred at pegging (R3) and podding (R4) stages.

Pod number was greater in late irrigated plants (40 plant^{-1}) when compared to early-irrigated plants (13 plant^{-1}) (Chapman *et al.*, 1993b). The effect of water stress during early reproductive phase (49-84 DAS) was studied in three cultivars (Chapman *et al.*, 1993b). In all cultivars there was a delay of at least 15 d in the time to the start of a rapid linear increase in pod biomass in the water stress treatment when compared to fully irrigated treatment.

Water deficit during the early reproductive phase (49-84 DAS) reduced both pod size and pod number. The decrease was associated with lower pod growth rates during water deficit (Chapman *et al.*, 1993b). Pod growth rates (PGR) were reduced to 0.22 Kg ha^{-1} (°Cd)$^{-1}$ in genotypes supplied with one-third of water as given to the control. Water deficit from 84 DAS reduced the number of pods produced from pegs. In all the cultivars studied by Chapman *et al.* (1993d), water deficit from 84 DAS reduced the pod number between 105 DAS and maturity, indicating pod abscission.

In a dry pegging zone, Sexton *et al.* (1997) and Bennet *et al.* (1990) observed that the percentage of pegs converted to pods was reduced from 81% in irrigated

(7-12% of gravimetric water content) to 57% in the water stressed treatments (< 0.5% of gravimetric water content).

2.5.2.4 Dry matter accumulation

Water deficits reduce dry matter production in vegetative components (Fourrier and Prevost, 1958; Ochs and Wormer, 1959; Su *et al.*, 1964; Lenka and Misra, 1973; Stansell *et al.*, 1976; Vivekanandan and Gunasena, 1976; Pallas *et al.*, 1979) as well as crop growth rate (Slatyer *et al.*, 1955).

In a study with four water stress treatments (Sarma and Sivakumar, 1989), where the net amount of water applied was 623, 522, 477 and 27 mm, total above-ground dry matter was 6000, 5900, 4200 and 1800 kg ha^{-1}, respectively. Similar decreases in dry matter under water stress conditions have been recorded by several researchers (Williams *et al.*, 1986; Nageswara Rao *et al.*, 1988; 1989; Wright *et al.*, 1991).

Crop growth rates (CGR) were recorded in a G x E study involving 36 genotypes grown in five environments. At 33% of irrigation, a CGR of 2.11 kg ha^{-1} $(°Cd)^{-1}$ was recorded as compared to 2.33 kg ha^{-1} $(°Cd)^{-1}$ in the irrigated control (Greenberg *et al.*, 1992). Similar decreases in CGR under water stress conditions have been recorded by Chapman *et al.* (1993b).

In contrast, transient moisture stress during the vegetative phase did not reduce the leaf area and vegetative weight at final harvest (Nautiyal *et al.*, 1999).

Nageswara Rao *et al.* (1985) also showed that maximum yields of groundnut could be achieved with decreased irrigation during early phases.

2.5.2.5 Pod yield and partitioning

A decrease in dry matter, flower, peg and pod number, and a delay in peg and pod initiation, under water stress conditions individually and in combination contribute to reductions in pod and seed yield. Reductions in pod yield were more pronounced when stress was imposed at the pod development and flowering phases than during the vegetative phase (Stirling *et al.*, 1989; Ravindra *et al.*, 1990; Wright *et al.*, 1991; Meisner and Karnok, 1992; Chapman *et al.*, 1993d).

Studies were conducted by Reddy and Reddy (1993), maintaining adequate water (actual evapo-transpiration (Eta) = maximum evapo-transpiration (ETm)), or severe water stress during the flowering and yield formation stages. Yields of 2345 to 2548 kg ha^{-1} in 1984, and 3009 to 3098 kg ha^{-1} in 1985 irrespective of moderate (60%) or severe (80%) depletion of available soil moisture at vegetative stages. When moderate or severe water stress was induced during the sensitive stages of flowering and pod development, 25% and 50% less groundnut yields were recorded, respectively. This study confirms again the acute sensitivity of flowering and pod development stages to water stress.

A drought screening study with 800 genotypes exposed to three combinations of timing and duration of drought and six to eight intensities of drought within each pattern of drought was conducted by Williams *et al.* (1986) at ICRISAT in India.

Pod yields decreased in a linear fashion as the intensity of drought increased (Fig. 2.4). In a comparison study with four cvs TMV 2, Robut 33-1, Nc Ac 17090, EC 76446 they identified that the largest differences between genotypes were due to effects of drought on their reproductive growth. TMV 2 produced highest pod yield in drought, with a harvest index 84% greater than that of EC 76446, the most susceptible genotype. They identified the ability to produce pods under drought (as in TMV 2) and the ability to recover from drought with greater pod growth (as in Robut 33-1) as two different mechanisms for higher yield under drought conditions.

In a study with 33 genotypes at the ICRISAT Sahelian center, Niamey, Niger, partitioning coefficient decreased from 0.52 (100% irrigation) to 0.24 (33% irrigation) as environments became less favourable (Greenberg *et al.*, 1992). They also identified genotypic differences for partitioning to pods. They observed that under drought already established pods have priority for partitioning of assimilates. Partitioning differences between genotypes were also attributed to ability of genotypes to initiate pod under drought conditions.

2.5.2.6 Root growth

Water stress reduces the uptake of nutrients and water per unit root mass (Marschner, 1988). This reduces the total amount of assimilate produced per unit of resources available that are translocated to roots. This decrease in assimilate translocation hampers root growth.

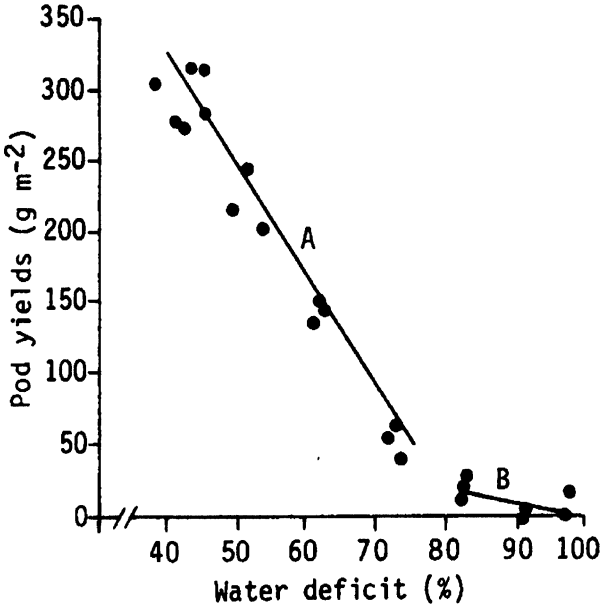


Fig. 2.4 The effects of drought intensity on pod yields in a long-duration drought. A : Y(0-70%) = 693 (±27.7) – 1.95 (±0.49) X; % var = 95; B: Y (80-100%) = 97 (±4.72) – 0.95 (±0.52) X; % var = 23. (Source: Williams *et al.*, 1986).

Root growth was studied in water stress treatments imposed by withholding irrigation for a 30 d period beginning at 20, 50, 80 or 110 d after sowing (Meisner and Karnok, 1992). Stress imposed at 20 and 50 DAS significantly reduced root growth compared to the well-watered treatment during the same period. No other stress period resulted in significant reductions. The later stress periods had no effect on root growth as 95% of total root length had been established by 80 DAS. Similar observations were made by McCloud (1974). This natural decline in root growth after 80 DAS has been attributed to change of sink from root to pod.

Differences in cultivar root volume, root dry weight, root length and number have also been recorded (Ketring *et al.*, 1982; Ketring, 1984). Rooting depth of Spanish cultivars varied between 1.9 (cv. Spancross) to 1.4 m (cv. Comet). In Virginia cultivars rooting depth varied between 0.2 (cv. Florunner) and 1.2 m (cv. Dixie runner). Rooting volume of Florunner was only 23 ml whereas cv. UF 77318 recorded 37 ml. These differences impart relative tolerance to water stress in groundnut and can be exploited in breeding tolerant groundnut genotypes.

2.5.3 Water stress effects on pollen, ovule and embryo

Reproductive development from meiosis to seed set is highly vulnerable to water stress, which can cause pollen sterility, spikelet death or embryo abortion of newly formed seed (Saini and Lalonde, 1998).

2.5.3.1 Pollen viability

Failure of fertilization due to inadequate pollen germination could be an important factor for poor peg formation during water stress conditions. Very few studies

have related pollen viability to peg and pod failure under water stress conditions in groundnut. In a study under irrigated conditions by Bhatia *et al.* (1984), the first formed flowers had about 70% pollen germination but this declined to 35% by 84 d after flowering in cvs J-11 and M-13. In the absence of irrigation, pollen germination was 25-35% during the 35-63 DAS in these cultivars. Pollination was impaired in the studies of Jain *et al.* (1997) when water stress was imposed during the flowering period.

Shen and Webster (1986) studied the effects of water stress on pollen of *Phaseolus vulgaris* L. and observed that the earlier stages of flower bud are most sensitive. Three stages of reproductive bud were subjected to water stress, tiny green buds (anthers containing tetrads or free microspores), green buds (anthers with uninucleate microspores with incipient exine formation), and white buds with tightly enfolded petals (anthers with binucleate pollen grains with well-developed exines). Plants in the tiny green bud stage recorded more aborted pollen grains and smaller pollen germination percentage than those at green bud or white bud stage. This study confirms that the green bud stage with microspores is most sensitive to water stress.

Increases of pollen sterility due to water stress has been reported in several cereal crops: wheat (Skazkin, 1961; Saini and Aspinall, 1981; Lalonde *et al.*, 1997); barley (Skazkin and Zavadskaya, 1957); rice (Sheoran and Saini, 1996) and maize (Downey, 1969). Water deficit is also known to cause anther abnormalities (Sheoran and Saini, 1996). Such studies have not yet been conducted in groundnut.

2.5.3.2 Ovule and Embryo

Studies have not been conducted in groundnut to see if water stress affects female fertility. Indeed, few attempts have been made to find out if water stress also affects female fertility in crops such as wheat (Saini and Aspinall, 1981), oat (Skazkin and Lukomskaya, 1962) or maize (Moss and Downey, 1971).

Water stress during embryo sac development in maize caused various abnormalities including a complete suppression of development (Moss and Downey, 1971). Depending on the severity and duration of stress, 15 to 43% of the ovules were abnormal, compared to just 2.5% in well watered plants. The failure of maize embryo sacs to develop into seeds was attributed to the failure of fertilised embryo sac to develop beyond 2-3 d because of poor embryo and endosperm development and a lack of seed coat differentiation (Westgate and Boyer, 1986). More research is needed to identify the precise causes for yield reduction under water stress conditions in groundnut.

2.6 EFFECT OF TEMPERATURE AND WATER STRESS ON GROUNDNUT

Water stress and high temperature stress are often found to occur simultaneously in the SAT. Research on their combined effects has been limited not only in groundnuts but also for crops in general. As described earlier both water stress and high temperature have detrimental effects on crop growth and development. Thus, questions remain unanswered as to whether the quantitative and qualitative effects of stress on groundnut production in rainfed areas are simply an effect of water stress or an additive effect of combined high temperature and water-stress.

The temperatures of the groundnut crop canopy and the soils in which crops are cultivated increase under water stress conditions when compared to those grown with full irrigation. Sivakumar and Sarma (1986) recorded the afternoon canopy temperature of plants under irrigated conditions to be 28.5°C, compared with 35°C in other treatments where three combinations of drought and soil temperature were imposed. Canopy, stem and pod temperatures were 8°, 10° and 10°C warmer, respectively in water stressed (33% of full irrigation) plants compared to the irrigated plots (Leong and Ong, 1983). Similar increases in canopy temperature due to water stress have been recorded by Sanders *et al.* (1985b), Musingo *et al.* (1989), and Craufurd *et al.* (1999).

In a study involving water stress imposed during the vegetative and reproductive periods of groundnut growth, soil temperatures at 0-50 mm depth (i.e. in the podding zone) were 0.7 to 4.9°C warmer in the water stressed than in irrigated plots (25°C). A greater increase in soil temperature, to about 36.2°C, was

recorded during the later stages of pod development, which is even more detrimental for pod yield. Similar increase in soil temperature under water stress conditions was also recorded by Ishag (1982) and Ravindra *et al.* (1990).

Although canopy temperature increased under water stress, Craufurd *et al.* (1999) did not find any significant interaction between temperature (27° and 34°C) and water stress (50 and 100%) for biomass or its components in groundnut. They also reported that temperature and water deficit have different and opposite effects on water use efficiency (WUE) and specific leaf area (SLA). Water deficit reduced water use and SLA, and increased WUE. High temperature had no effect on water use, but decreased WUE and increased SLA.

As well as any decrease in biomass or yield, any loss of quality will also greatly reduce groundnut market value. Musingo *et al.* (1989) suggested that water stress (period longer than 30 d) and high soil temperature (around 28°C) cause an increase in accumulation of carbohydrate and polypeptides, which may enhance the *Aspergillus* invasion and aflatoxin production.

The combined effect of extreme temperature and water stress on wheat grain yield was described by Nicolas *et al.* (1984). Water stress alone significantly reduced final grain weight. The reduction was greater when water stress was applied late rather than the early period of during endosperm cell division (reductions of 37% and 24%, respectively, relative to the control treatment). High temperature alone also significantly reduced final grain weight but the reduction was smaller (5% in early and 13% in late periods) than that caused by water

stress treatments. The combined effect of water stress and high temperature was much more pronounced than that of each treatment alone, as final grain weight was reduced by 49% and 60% when the combined treatment was applied during the early and late periods of cell division, respectively.

These reviews of literature leave no doubts that further studies are essential to account for the combined effects of high temperature and water stress in groundnut. Such research will help to identify the quantitative and qualitative effects of stress that are required to better target future groundnut breeding strategies in the SAT.

2.7 Crop Simulation models

Crop modelling can be defined as the dynamic simulation of crop growth by numerical integration of constituent processes with the aid of computers (Sinclair and Seligman, 1996). Several authors have reviewed the advantages and shortcomings of crop simulation models (Moorby, 1987; Curry *et al.*, 1990; Baker, 1996; Boote and Jones, 1988; Monteith, 1996; Sinclair and Seligman, 1996; Porter and Jamieson, 1999). The efficiency of a simulation exercise depends on the objectives for which the crop simulation model is being used. A simple water balance model was found superior to complex simulation models of cotton (*Gossypium hirsutum*) such as COTTAM and GOSSYM in approximating crop water stress and field water balance (Asare *et al.*, 1992). An empirical equation was found superior to the complex CERES model in predicting annual potential wheat (*Triticum aestivum* L.) yields in Mexico (Bell and Fisher, 1994). SOYGRO, a mechanistic model for soyabean, was found inferior to a simple average of a sample in predicting soyabean yield in an unsampled population (Colson *et al.*, 1995).

Simulation models can be used as research tools, management tools and policy tools. As a research tool, simulation models can be used to model specific crop process and to design experiments to fill in gaps in knowledge. Along with aiding decision making for crop production under current conditions, crop models also help to identify the crop sensitivity to future predicted climates (Curry *et al.*, 1990; Holloway *et al.*, 1995; Semenov and Porter, 1995; Luo and Lin, 1999; Saseendran *et al.*, 2000). The model SOYGRO has been used to study the potential impact of global climate change on soyabean production (Curry *et al.*,

1990). Sensitivity of models to changes in temperature and photoperiod have been studied in soyabean and groundnuts (Boote *et al.*, 1992; Hoogenboom *et al.*, 1990). As it is difficult to simulate the future climates under field conditions, crop models can act as surrogates for designing future crop genotypes and cropping systems. This may help in identifying areas for crop improvement in order to sustain crop yields in predicted harsh climates of increased temperature, increased CO_2 and decreased water availability.

Crop models not only help in designing strategies for yield improvement at a field scale, but can also work as a tool for predicting regional and national food grain yields (Meinke and Hammer, 1995) when combined with Geographic Information Systems (GIS) (Lal *et al.*, 1993; Thornton *et al.*, 1997; Hartkamp *et al.*, 1999). A combination of crop models and GIS, such as AEGIS (Calixte *et al.*, 1992; Calixte, 1992) and AEGIS/WIN (Engel *et al.*, 1997) can help in identifying the gaps from field to regional to national scale in order to realise the potential crop yields in the tropics.

Advances in crop models can be attributed to both an increase in understanding of crop physiology and an increase in computer processing power. An increase in understanding of crop physiology genetics is enabling crop modellers to use this knowledge to accurately predict crop yields with genotypic specificity. "Gene Gro", a gene based simulation model has been developed that integrates action of seven genes into a common bean model (White and Hoogenboom, 1996, Hoogenboom *et al.*, 1997). The results from this study support the use of genotype specific information to represent cultivar differences in crop models.

With increased understanding of genetics and physiology, a progressive improvement is probable in crop models. This continuous improvement needs an alteration of the complex and cumbersome source code of crop models, currently in FORTRAN. To overcome this, modular (Porter *et al.*, 2000) or object oriented approach (Evert and Campbell, 1994; Pan *et al.*, 2000) is becoming popular to handle the improvements to crop models. Large data sets are available from experiments that are difficult to handle. In certain experiments, the relation between the inputs and outputs cannot be well defined based on the current level of statistical and modelling knowledge base. Artificial neural networks offer a solution due to their dynamic state response to inputs and ability for supervised learning. Neural networks can be viewed as a computer system with interconnected processing elements similar to the neuron network found in brain (McClelland, 1986). These artificial neural networks are beginning to be used in the next generation of crop models (Elizondo *et al.*, 1994; Parmar *et al.*, 1997).

Rapid advance in Internet technology is also moving the current PC based crop models to the Internet, thus enabling access to many individual researchers, model developers and farmers. These web-based models are developed using JAVA, an object oriented programming language. Even though the examples of such crop models are few (Pan *et al.*, at http://th190-50.agn.uiuc.edu/Simulator), an increase in spread of the Internet in the tropics and semi-arid tropics would enable farmers and researchers to gain access to these otherwise elusive crop models.

This revolution would enable farmers to learn the deficiencies in their management practices. Although not internet based, two examples are worth mentioning here to show how farmers can learn efficient crop production and management from crop models. The SIRATAC model for cotton pest management in Australia (Ives *et al.*, 1984) and the EPIPRE model for wheat pest management in The Netherlands (Rabbinge and Rijsdijk, 1987) have a central processing centre. These centers receive data from farmers and run the simulations to provide growers with updated pest management recommendations. The simulated recommendations from model improved the pest management along with increased membership. However membership declined later as the growers felt they had learned the lessons of the models and could now manage on their own (Weiss, 1994).

2.8 CROP SIMULATION MODELS FOR GROUNDNUT

2.8.1 PEANUTZ

PEANUTZ is a first generation FORTRAN computer program developed to simulate the growth and development of groundnuts from the date of planting until harvest (Young *et al.*, 1979). The model begins by simulating the time of seedling emergence. Then, for each day of the growth cycle, it simulates the weight of photosynthate produced, the maintenance respiration, the change in peg mass, and peg numbers, the flower count, and the change in leaf and stem mass. Growth respiration for each plant part is predicted within blocks simulating growth of that part. This model helped to identify areas for further research to improve the understanding of groundnut growth and development and laid the future for developing more sensitive and complicated models for groundnut.

2.8.2 PNUTGRO

The groundnut model PNUTGRO is a process level model developed by an interdisciplinary research team in the USA to simulate growth and yield (Boote *et al.*, 1986; 1989). The major components of the model are vegetative and reproductive development, and carbon, nitrogen, and water balance modules. The model initiates the simulation of development immediately after sowing. It predicts the periods from sowing to emergence; to first full leaf expansion; to the start of flowering; to first pod occurrence; to the beginning of seed filling; to the end of leaf growth and expansion; to the end of pod growth and expansion; physiological maturity; and harvest maturity (Fig.2.5). The model also predicts leaf area development and vegetative node formation on the main stem.

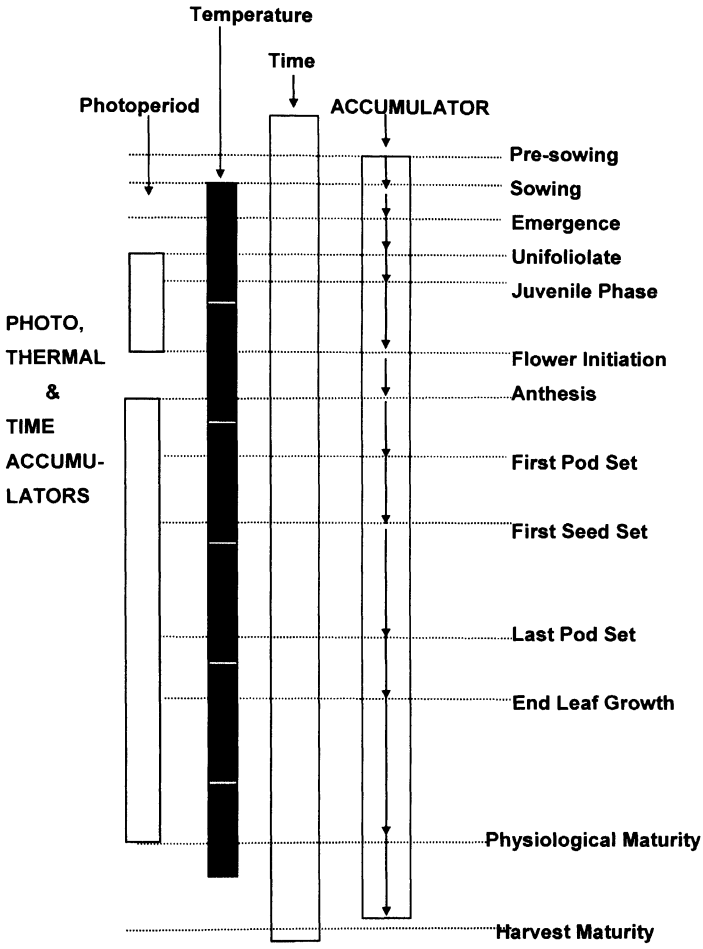


Fig. 2.5 Vegetative and reproductive development in PNUTGRO, represented by successive development stages, as a function of photoperiod and/or temperature, represented by accumulator bars. (As shown here the stage from sowing to unifoliolate leaves is a function of temperature and time only, while most of other cases are a function of temperature, photoperiod, and time). (Source: Hoogenboom *et al.*, 1992).

Each of the stages mentioned has a optimum thermal time value. For most stages in the model only a temperature effect is included, based on temperature response curve, rather than a degree day concept as used in many other models. It is assumed that development will occur at an optimum temperature or maximum relative rate of unity (photothermal days per calendar day) for a given optimum range. The model uses two kinds of response functions for crop development: (1) a linear function for the vegetative stage progression defined by a base temperature (T_b), optimum temperature (T_o), and maximum temperature (T_m); and (2) a full *sine* function for reproductive development which is a function of base temperature and optimum temperature. For vegetative stages the cardinal temperatures are proposed as:

$$T_b = 13.5°C,\ T_o = 28 - 35°C \quad \text{and } T_m = 55°C$$

Three different *sine* functions are used to calculate physiological days from emergence to flowering (T_b = 9.5°C and T_o = 27.2°C); flowering to pod-initiation (T_b = 9.5°C and T_o = 25.8°C); and beginning seed growth to physiological maturity (T_b = 5.0°C and T_o = 25.9°C).

The model predicts total canopy photosynthesis on a daily basis as a function of daily photosynthetically active radiation, converted from daily total solar radiation. After daily photosynthesis is calculated, daily maintenance respiration is subtracted to account for the daily turnover of proteins. Partitioning to vegetative and reproductive structures is determined based upon development phase. Values for LAI are calculated based upon dry matter partitioned to leaves and leaves abscised due to senescence. Leaf senescence is predicted as a function of plant age. The daily soil water balance in the model uses Ritchie's (1985) one-

dimensional soil water balance approach. Evapo-transpiration is estimated using the procedures defined by Ritchie (1972). Growth of new roots is distributed over the various soil layers as a function of a root preference factor for each layer, the amount of extractable water in each layer and whether root progression has reached a given layer.

The model needs inputs of location, weather, soil and management data. Local variables are latitude and longitude (radians). Daily weather variables are solar radiation (MJ m^{-2}), rainfall (mm), and maximum and minimum temperature (°C). In addition to these data, the model also uses crop-specific and cultivar-specific coefficients.

The PNUTGRO model predicts the timing of vegetative and reproductive growth stages from emergence to physiological maturity, daily growth increments of plant components, leaf area index, specific leaf area, root distribution in the soil, percent nitrogen in the crop canopy, final yield, yield components, and harvest index (Fig. 2.5). In addition, daily soil water balance components, namely soil evaporation, transpiration, drainage, and surface runoff are also estimated.

Further details about PNUTGRO are given by Boote *et al.* (1998, 1999).

2.8.3 QNUT

The framework and the logic employed in the QNUT model of Hammer *et al.* (1995) are presented in Fig. 2.6. The main objective of the model is to predict pod yield as the product of biomass and harvest index (HI). Daily increase in

total above ground biomass (ΔB_T) is required to predict pod yield and is calculated as:

$$\Delta B_T = R \times I \times RUE \times RT \quad [2.1]$$

$$I = 1.0 - \exp(-k \times LAI) \quad [2.2]$$

where
- R = incident solar radiation
- I = fraction of the radiation intercepted by the crop
- RUE = radiation use efficiency
- RT = relative transpiration
- k = extinction coefficient of canopy

Crop leaf area is required to predict biomass accumulation and is calculated as the product of leaf area per plant (PLA) and plant density. A power function was fitted to the progression of effective leaf number (ELN) on main stem nodes (NODES), where:

$$ELN = 0.1808\ (NODES)^{2.443} \text{ for nodes } </= 15 \quad [2.3]$$

When NODES exceeded 15, ELN is incremented by 19 leaves for each new node. The potential increment in leaf area is calculated as the product of leaf size (individual leaf area and increment in ELN). Phenological development is based on accumulation of thermal time. A base temperature of 9°C and optimum temperature of 29°C (temperatures above this cause reduction in branching, thus reducing leaf area growth) were used to calculate the thermal time for different phenological stages. Maturity was taken as the estimated time of accumulation of maximum biomass.

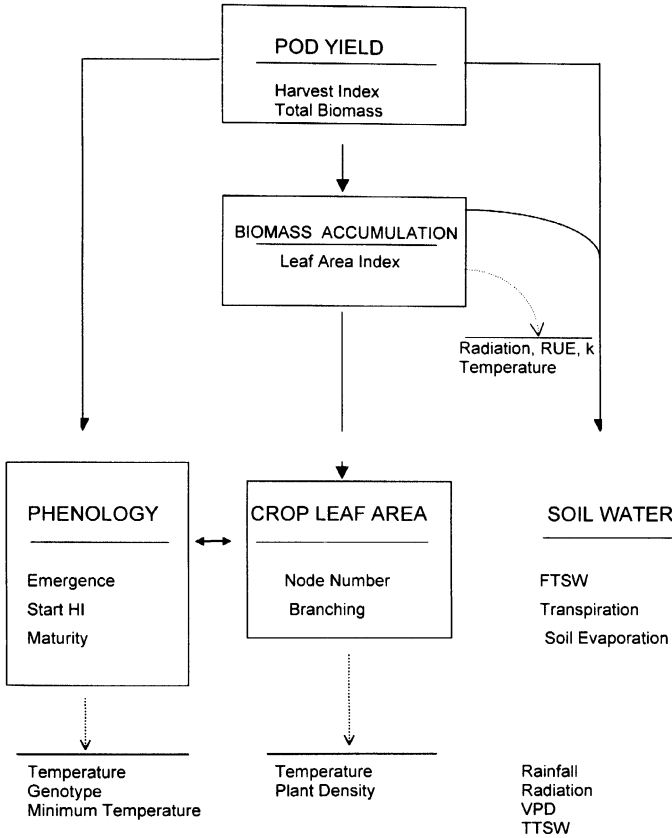


Fig.2.6 Schematic representation of the framework and top-down logic used in the QNUT model. Boxes represent major modules. Solid arrows denote logical connections and broken arrows denote connections to climatic, soil, management, and crop specifications. (RUE is the efficiency with which the intercepted radiation was used to produce biomass; k is the extinction coefficient of the canopy; FTSW is the fraction of transpirable soil water; VPD is vapour pressure deficit; TTSW is total transpirable soil water). (Source: Hammer *et al.*, 1995).

Values for HI increase linearly with time. A linear regression defined the harvest index slope and time of onset of HI increase for each data set whereby:

$$HI_t = Hi_{t-1} + \Delta HI \quad [2.4]$$

$$\Delta B_p = B_{v,t-1} [Hi_t / (1- Hi_t)] - B_{p,t-1} \quad [2.5]$$

$$B_{p,t} = B_{p,t-1} + \Delta B_p \quad [2.6]$$

$$B_{v,t} = B_{v,t-1} + \Delta B_T - 1.5\Delta B_p \quad [2.7]$$

where, Hi_t = Harvest Index on Day t

Hi_{t-1} = Harvest Index on Day t-1

ΔHI = slope of Harvest Index increase (day^{-1})

ΔB_p = change in pod biomass

$B_{v,t-1}$ = vegetative biomass on Day t-1

$B_{p,t-1}$ = pod biomass on Day t-1

$B_{p,t}$ = pod biomass on day t

ΔB_T = increase in the above ground biomass ($g\ m^{-2}\ day^{-1}$)

2.9 PERFORMANCE OF GROUNDNUT CROP MODELS

The PNUTGRO and QNUT models were used by Bell and Wright (1998) to calculate cumulative thermal time from sowing to maturity in groundnuts grown in the humid tropics of Indonesia, in the SAT of north-west Australia, and in humid coastal and inland elevated areas of Australia. Neither model was able to adequately predict degree day accumulation across average temperatures ranging from 22.5° to 30.5°C and thus could not predict the occurrence of key crop growth stages accurately. The models also had considerable difficulty in predicting reproductive maturity across environments.

The limitations in the QNUT model were thought to reflect an inability to cope with reduction in rate of development at supra-optimal temperatures. In PNUTGRO predicted developmental rates were too high at high temperatures (>31°C) and too low at moderate to cool temperatures (<27°C), which could reflect differing developmental responses to temperature by and within both vegetative and reproductive components.

The model PNUTGRO has been widely used to study the effects of various abiotic and biotic stress factors on groundnut growth and development. Singh *et al.* (1994a) used the model to evaluate crop response to water availability, sowing dates and seasons in India. Changes in vegetative growth stages, total dry matter accumulation, growth of pods and seeds, and soil moisture were predicted accurately. Predicted pod yields were strongly correlated (r^2=0.90) with observed yields. They concluded that under biotic stress-free situations, the model PNUTGRO can be used to predict groundnut yields in different environments as determined by season, sowing date and moisture regimes. PNUTGRO was also evaluated for crop response to plant population and row spacing using field data of groundnut crops sown at varying plant populations between 10 to 40 plants m^2 and at row spacings of 20, 30 and 60 cm. The model predicted the occurrence of vegetative and reproductive stages, canopy development, total dry matter production and its partitioning to seeds and pods accurately.

Kaur and Hundal (1999), using the results obtained from PNUTGRO for five consecutive crop seasons found satisfactory predictions of phenology, growth

and groundnut yield and hence concluded that the model can be used for forecasting growth and yield of groundnut in Punjab state of India. In their study, the phenological events showed deviations from observed times of only –3 to +3 days for flowering, -3 to +2 days for pegging and –4 to +2 days for physiological maturity of the crop. The model predicted pod yield from 89 to 111% and seed yield from 90 to 110% of the observed yields.

In summary, PNUTGRO, once calibrated for a given location, can effectively predict groundnut yields under a given set of biotic stress-free conditions. However, in addition to water stress and plant competition, the areas where groundnut is cultivated are also prone to extremes temperature. The information on groundnut responses to temperature is meager or unavailable (Boote *et al.*, 1998) and the model has not been tested at supra-optimal temperatures. It is in these circumstances and especially in the SAT that reliable models are needed.

CHAPTER 3

EFFECTS OF TEMPERATURE AND WATER STRESS ON GROUNDNUT IN CONTROLLED ENVIRONMENTS

3.1 INTRODUCTION

The groundnut crop cultivated in the semi-arid tropics rarely achieves its full genetic potential due to limitations imposed by environmental stresses. In these semi-arid environments of the world, which contribute to 90% of global groundnut production, the occurrence of high temperature and water stress are not exclusive of one another (Nix, 1975; Kramer, 1980). The severity of these environmental stresses is likely to increase in the future based on climate predictions (IPCC, 2000).

The groundnut crop is exposed to both mid-season and end-season water stress, which may coincide with flowering and pod development, respectively, the periods most sensitive to water stress (Kulkarni *et al.*, 1988; Jain *et al.*, 1997; Nautiyal *et al.*, 1999). The flowering period in groundnuts is sensitive also to high temperature episodes (Vara Prasad *et al.*, 2000a). Temperature is the dominant factor controlling the rate at which groundnut plants develop (Fortanier, 1957; De Beer, 1963; Cox and Martin, 1974; Cox, 1979). Studies conducted so far have concentrated mostly on the effect of water stress in groundnut, rather than high temperature effects, even though the manner in which high temperature affects plants is probably better understood (Kramer, 1980). Experimental studies have not been carried out in groundnuts to study the interaction of these stresses. Such studies are also few in other crops (e.g. maize - Schoper *et al.*, 1986; wheat – Nicolas *et al.*, 1984). In this experiment the combined effect of water stress and high temperature on the growth, development and yield of groundnuts was investigated using controlled environments.

The objectives of this study were: (1) to investigate the effects of water stress and high temperature on the growth, development and yield of groundnut; and (2) to investigate the effects of an interaction between water stress and high temperature on groundnut yield.

3.2 MATERIALS AND METHODS

3.2.1 Growth conditions

Seeds of groundnut cultivars ICG 796 and ICGV 86015 treated with Apron Combi 453 FS (Ciba, Agriculture, Cambridge, UK) were sown in module trays filled with compost. After germination, seedlings of similar size were transplanted to pots 0.75 m deep and 0.30 m diameter (Plate 3.1a), containing 17 kg of sterilized rooting medium. The rooting medium comprised sand, gravel, vermiculite and loamless peat compost mixed in proportions of 4:2:2:1, by volume, respectively. A commercial controlled-release fertiliser (0.15 kg kg^{-1} N, 0.10 kg kg^{-1} P, 0.12 kg kg^{-1} K, 0.02 kg kg^{-1} MgO plus trace elements; Osmocote Plus, Scotts UK Ltd, UK) was incorporated into the mixture at the manufacturer's recommended rate of 5 g L^{-1}. Seeds were not inoculated with rhizobia and so plants were dependent on inorganic nitrogen. All pots were soaked and drained for 24 h before seedlings were planted; there after they were hand-watered based on the water stress treatment. The sides of the pot were painted white to reduce radiative heating.

The experiment was carried out in a poly-tunnel at Plant Environment Laboratory, Shinfield, University of Reading, UK (Plate 3.1a). A photo- and thermo-period of 12 h d^{-1} (0800 to 2000 h) was maintained in the poly-tunnel throughout the experimental period. A manually operated black-out facility controlled the photoperiod. A plastic bubble (Plate 3.1b) was constructed in the poly-tunnel to

impose high temperature treatments. Thin, 40-gauge (40 μ) polythene, with 95% transmission, was used to minimise differences in radiation levels between plants in the poly-tunnel and those in the plastic bubble. Air temperature and humidity in the poly-tunnel and bubble were measured with screened and aspirated copper-constantan thermocouples positioned at the top of plant canopy. Readings were taken at 10 s intervals and means of successive 10 min periods were stored using a data logger (Delta-T Devices, Ltd, Cambridge, UK). Carbon dioxide fluctuated at near ambient concentrations (360 ppm) and relative humidity during the day was controlled by automatic water sprinklers and ventilation to give a VPD close to 2 kPa in both tunnel and bubble. The poly-tunnels transmitted about 75% of incoming photosynthetically active radiation (PAR) during the experiment period in 1998.

All plants were healthy and there were no serious pest or disease problems. Torque (*a.i.* Fenbutatin Oxide) controlled a mild incidence of red spider mite (*Tetranychus urticaei Koch.*) at 80 DAS.

3.2.2 Treatments

The experiment consisted of a factorial combination of three water stress treatments, two temperature treatments and two genotypes. Each treatment combination was replicated four times.

The genotypes used in the study, ICGV 86015 and ICG 796, are Spanish bunch types requiring about 120 d for maturity. ICGV 86015, which originated from a cross between ICGS 44 and TG 2E, was released in 1993 as an early maturing, high-yielding line. It is particularly well adapted to rainfed conditions. ICG 796,

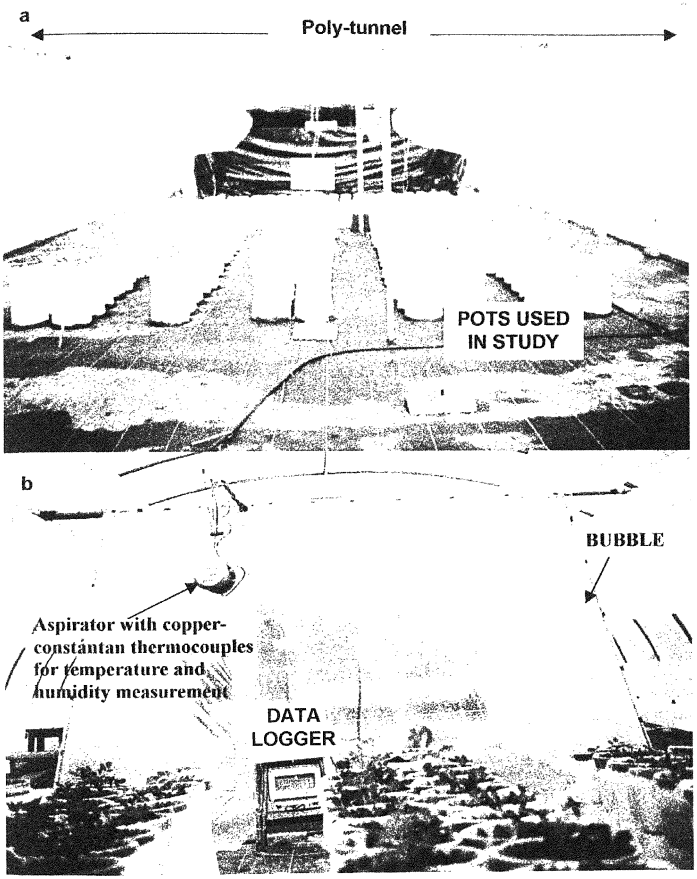


Plate 3.1 Photographs showing (a) inside of poly-tunnel with special pots used in the study and (b) bubble inside poly-tunnel used to impose high temperature treatments.

which is popularly known as Punjab 648, performs well under irrigated conditions. Genotype ICGV 86015 was classified as moderately tolerant to water stress and high temperature, while ICG 796 is susceptible to both the stresses.

Water stress treatments were; D1 – irrigated to maintain field capacity (FC, where the available soil moisture (ASM) is 100% at field capacity) throughout the study; D2 – early water stress (40% ASM) from flowering to pod initiation; and D3 – late water stress (40% ASM) from pod initiation to harvest. Available soil moisture (ASM) is defined here as the difference in soil moisture percentages at field capacity (FC) and permanent wilting point (PWP). In both water stress treatments irrigation was withheld 7 d prior to the start of the treatments. The aim was to reduce the moisture content to 40% ASM when the treatments started. Pots were weighed daily, from 7 d before the start of the treatment, with a Mettler PM30-K balance weighing up to 32 kg with an accuracy of 1g. The amount of water used each day was determined, and pots were re-watered to maintain them at the required ASM level. Amount of water lost on each day was considered as daily evapo-transpiration (ET).

The rooting medium had a water holding capacity of 13.5% w/w at FC measured at pressure of $^1/_3$ bar, and PWP of the medium was 4.2% w/w measured at a pressure of 15 bars, using a pressure plate apparatus. Figure 3.1 indicates that the rooting medium holds 13.5% w/w of moisture at a suction of 50 cm H_2O. The measured saturated hydraulic conductivity of the medium was 1.14×10^{-3} m s^{-1}.

Groundnut plants were also exposed to two temperature treatments: T1 - optimum temperature of 28°/22 °C (day/night); and T2 - high temperature of

40°/22 °C (day/night) for a period of 10 d starting when the genotypes reached 50% flowering. The high temperature treatment (T2) was imposed by transferring four plants from each of the water stress treatments into the plastic bubble erected in the poly-tunnel. These T2 plants were grown at 28°/22°C for the rest of the growing period.

3.2.3 Observations and data analysis

Plants were harvested at 20 DAS, 50% flowering (R1- 35 DAS), pod initiation (R3 – 50 DAS) and finally at 87 DAS. At each harvest plant height, leaf number and total leaf area, peg and pod numbers, and root length (mesocotyl to tip of main root) of every individual plant were recorded. Plants were separated into leaves, stems, roots, pegs and pods. The respective dry weights of leaves, stems, roots and pods per plant were recorded after oven-drying these components at 80 °C to a constant weight. Total dry weight (excluding senesced leaves and roots) and pod harvest index (ratio of pod to total dry weight) were calculated from the weight of individual components. Values for pod dry weight in the study were adjusted by multiplying recorded data by a factor of 1.65 to allow for the oil content of the seeds (Duncan *et al.*, 1978). Data on plant dry weight were log transformed before analysis to ensure homogeneity of variances. Water use efficiency (WUE) was calculated as the ratio of total above ground biomass dry weight (including pods) to total ET. Root weights were not included in the biomass for WUE to enable comparison with the field study.

Duration (d) from sowing to appearance of first fully opened flower, 50% flowering (R1), first peg (R2) and to pod initiation (R3) – when tip of peg was

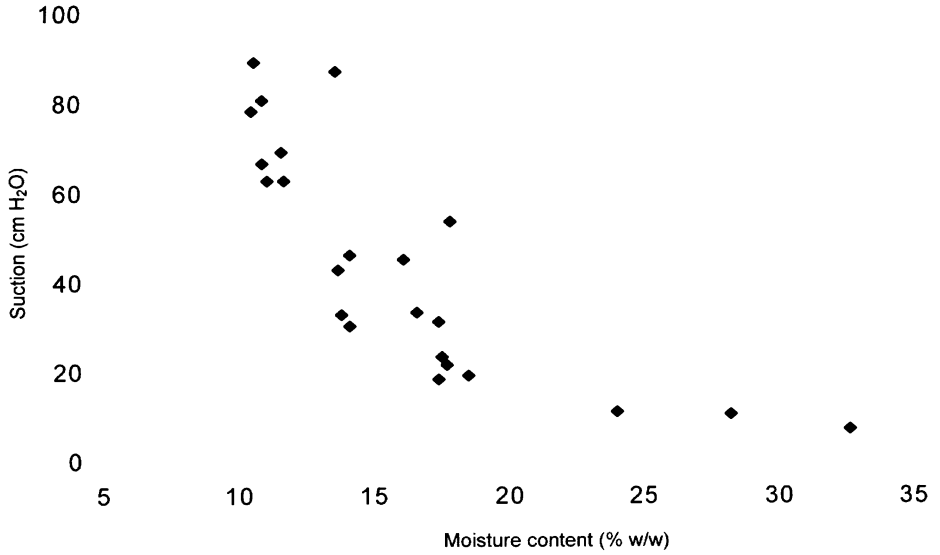


Fig 3.1 Relation between moisture content (% w/w) and suction (cm H_2O) of the root growth medium (PEL mix) used in the study.

more than twice the diameter of peg (Boote *et al.*, 1982), were recorded on all plants. Daily flower counts were also made on all plants during the experimental period. At each harvest the total number of pegs and pods per plant were counted. The proportion of flowers setting pegs (peg-set) was calculated as the ratio of peg number to total cumulative flower number. The proportion of flowers setting pods (pod-set) was calculated as the ratio of pod number to total cumulative flower number. Similarly, the proportion of pegs forming pods (peg-pod) was calculated as a ratio of pod to peg number. The data on percentage peg-set, pod-set and peg-pod were subject to angular transformation before analysis to ensure homogeneity of variances.

Data was analysed using ANOVA in GENSTAT 5 (Genstat 5 Committee, 1997) as a factorial design, replicated four times. ANOVA tables for observations made at 50 and 87 DAS are in Tables 3.1 and 3.2. Significance of SED values is depicted with * or ** or *** which correspond to probability (p) levels of $p<0.05$, $p<0.01$ and $p<0.001$, respectively. In graphs, SED is represented as vertical bar.

3.3 RESULTS

3.3.1 Environment

The daily maximum and minimum temperatures were fairly constant about an average maximum and minimum of 28.8°C (±SE 0.09) and 22.5°C (±SE 0.04), respectively (Fig.3.2). The 10 d high air temperature treatment (T2) had a mean day temperature of 36.7°C (±SE 0.6), 3°C below the target temperature of 40°C. The average water status of the mixture was 60% of ASM in D2 and 40% of ASM in D3 (Fig 3.3). The PAR received during the experimental period averaged 565 (±SE 0.01) μmoles m^{-2} s^{-1}. During the 10 d high temperature period relative humidity (RH) under optimum conditions averaged to 79.5% (±SE 0.75) giving a vapour pressure deficit (VPD) of 0.84 kPa, while in the bubble with hot air temperature RH was 71.1% (±SE 0.70) with a high VPD of 1.71 kPa.

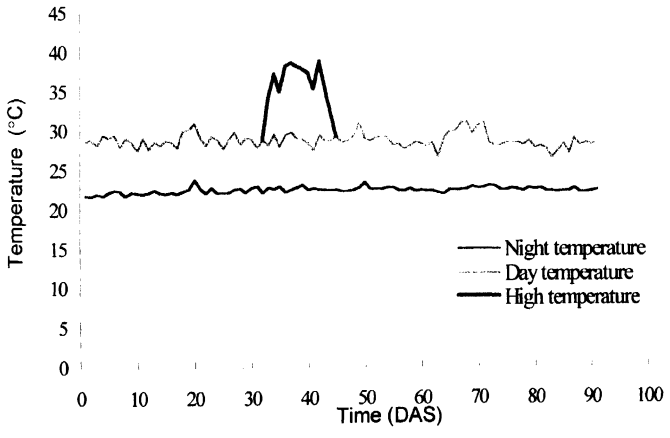


Fig. 3.2. Daily record of maximum and minimum temperatures during the crop growth period.

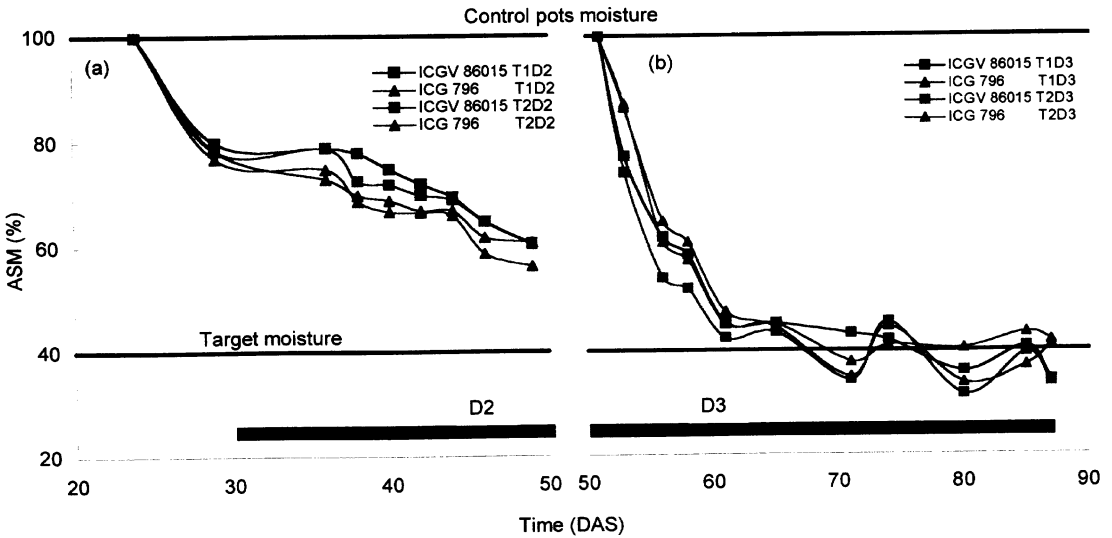


Fig. 3.3 Moisture content curves in pots imposed with (a) early water stress (D2) from flowering to pod initiation and (b) late water stress (D3) from pod initiation to harvest.

3.3.2 Growth harvests

Two harvests were made in this experiment, one at pod initiation (50 DAS) and the other at maturity (87 DAS). The harvest at 50 DAS, at the end of the high temperature and early water stress treatments, was taken in order to examine the interaction between high temperature and water stress.

At 50 DAS there were significant main effects of water stress, but few water stress x cultivar interactions (Table 3.1). There were significant effects of temperature and temperature x water stress interactions. There was, however, little difference between cultivars and only one temperature x cultivar interaction for pod number.

At final harvest (87 DAS) there were significant effects of water stress, cultivar and water stress x cultivar interactions. The main effects of temperature were also significant, but there were no interactions between water stress and cultivar with temperature (Table 3.2).

The results described below have therefore been divided into three main sections: cultivar effects, water stress x cultivar interactions (at final harvest), and temperature x water stress interactions (at 50 DAS).

Table 3.1 Analyses of variance with mean squares and treatment significance for growth and development parameters recorded at 50 DAS.

Source	df	PH	MSN	LN	LA	LWT	SLA	SWT	VWT	PN	PWT	BM	WUE	RWT
Replicate	3	12***	1.3	122	111624	2	707	0.9	8	21	0.3	11	0.07	0.3
Water stress (WS)	1	693	66***	3655***	3677495***	84***	532	35***	260***	28***	1.1*	294***	3.6***	2.5*
Temperature(T)	1	0.03	0	10	10953	0.2	23	2.4*	13*	80*	1.3*	23*	0.12	0.9
Cultivar (CV)	1	72	0	1081**	42391	1	574	0.4	8	16	0.01	8	0.04	2.7*
WS x T	1	3	3	153	351569**	10***	193	2.5*	44***	3	0.01	46**	0.16*	1.5
WS x CV	1	20	0	231	181523*	4.5*	210	1.4	11	39	0.01	11	0.14*	0.2
T x CV	1	17	1	15	1491	0	132	0.1	0.4	102*	0.6	0.01	0.0	0.1
WS x T x CV	1	1	0.5	36	90487	0.1	704	1.12	0.5	19	0.2	0.08	0.0	0.05
Residual	21	24	1.2	80	31010	0.6	268	0.5	59	14	3.4	3.4	0.03	0.45

(*, **, *** indicate significance at 0.05, 0.01 and 0.001 levels of probability, respectively; df = degrees of freedom, PH = plant height (cm), MSN = main stem node number, LN = leaf number, LA = leaf area (cm^2), LWT = leaf weight, SLA = specific leaf area ($cm^2\ g^{-1}$), SWT = stem weight, VWT = vegetative weight, PN = pod number, PWT = pod weight, BM = biomass, WUE = water use efficiency ($g\ L^{-1}$), FLN = flower number, RWT = root weight; all weights are g $plant^{-1}$ and all numbers are per plant).

Table 3.2 Analyses of variance with mean squares and treatment significance for growth and development parameters recorded at 87 DAS.

Source of variation	Df	PH	MSN	LN	LA	LWT	SLA	SWT	VWT	PN	PWT	BM	WUE	FLN	RWT
Replicate	3	6	0.8	363	61961	3	629.1	4	43	71	80	204	0.5	610	18
Water stress (WS)	2	420***	45***	5344***	11566556***	287***	8260***	557***	2963***	988***	1948***	9709***	28***	36552***	258***
Temperature (T)	1	14	4	1092*	1429051*	31*	164	36*	388***	52	13	549	1.8*	9185**	66*
Cultivar (CV)	1	65	19**	6142***	8107111***	284***	9466***	330***	3477***	3502***	302	1729**	3.7**	102675***	573***
WS x T	2	9	4	319	402208	7	225	16	87	66	5	77	0.3	2046	8
WS x CV	2	54	0.3	689*	1920937***	56***	686	87***	894***	277**	73	1038**	3.2**	5339*	171***
T x CV	1	4	0.3	165	87286	3	69	6	55	0.7	13	15	0.0	48	10
WS x T CV	2	12	3	335	340190	7	244	13	81	33	8	137	0.4	467	8
Residual	33	28	2	198	222484	5	388	6	29	1392	97	161	0.4	1063	10

(*, **, *** indicate significance at 0.05, 0.01 and 0.001 levels of probability, respectively; df = degrees of freedom, PH = plant height (cm), MSN = main stem node number, LN = leaf number, LA = leaf area (cm^2), LWT = leaf weight, SLA = specific leaf area ($cm^2\ g^{-1}$), SWT = stem weight, VWT = vegetative weight, PN = pod number, PWT = pod weight, BM = biomass, WUE = water use efficiency ($g\ L^{-1}$), FLN = flower number, RWT = root weight; all weights are $g\ plant^{-1}$ and all numbers are per plant).

3.3.3 Cultivar differences

No significant difference in the phenology of the two cultivars could be observed under control (T1D1) conditions. Both ICGV 86015 and ICG 796 had their first flower at 28 DAS, reached 50% flowering by 35 DAS, and had their first peg (R2) and pod (R3) at 39 and at 50 DAS, respectively. High temperature treatment did not alter these dates.

Cultivar differences were significant ($p<0.05$) only at 87 DAS for biomass. Cultivar ICG 796 recorded higher vegetative weight and in turn higher biomass than ICGV 86015 (Table 3.3). Similar differences were also recorded for leaf and stem weights. However, there were no significant differences in pod weights among cultivars due to higher HI ($p < 0.01$) in ICGV 86015 (0.54) than ICG 796 (0.39).

Table 3.3 Cultivar differences between ICG 796 and ICGV 86015 for dry weights of leaf, stem, vegetative, biomass and HI observed at 87 DAS. Values in parenthesis are original values and analysed based on log transformed values.

Character	ICG 796	ICGV 86015	SED
Leaf weight (g pl^{-1})	1.11 (13.90)	0.94 (9.04)	0.025***
Stem weight (g pl^{-1})	1.11 (14.65)	0.95 (9.4)	0.025***
Vegetative weight (g pl^{-1})	1.57 (41.4)	1.37 (24.4)	0.023***
Biomass (g pl^{-1})	1.79 (67.4)	1.72 (55.4)	0.029*
HI (ratio)	0.30	0.54	0.011**

The principal difference between the two cultivars was in the flower production. Cultivar ICGV 86015 produced 55% more flowers than ICG 796, and this resulted in 36% more pegs, and 38% more pods (Table 3.4). This was associated with a faster rate of flower production per day (Fig. 3.4), particularly in the first 30 d after flowering. Pod size was not significantly different.

Table 3.4 Cultivar differences in peg and pod number, and pod set of ICG 796 and ICGV 86015 observed at 87 DAS. Values in parenthesis are original values and analysed based on log transformed values.

Character	ICG 796	ICGV 86015	SED
Flower number	74	167	9.4***
Pod number (pl^{-1})	28	45	1.8***
Pod weight (g pl^{-1})	1.36 (25.9)	1.45 (27.9)	0.047^{NS}
Pod set (%)	39.8	32.9	3.6***

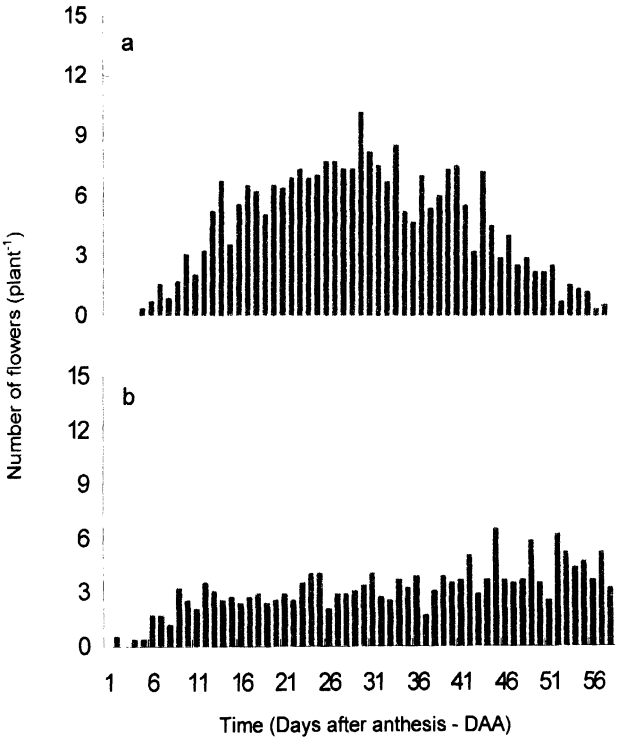


Fig. 3.4 Daily flower production in groundnut genotypes, ICGV 86015 (a) and ICG 796 (b).

3.3.4 Water stress effects and interaction with cultivars

The two cultivars differed in their sensitivity to water stress. The differences observed at 50 DAS for early water stress persisted until final harvest. Hence, only water stress effects at final harvest (87 DAS) are described here.

3.3.4.1 Water use and water use efficiency

Water use is described here as the total amount of water lost through evapo-transpiration (ET). Cumulative ET and WUE at 87 DAS are given in Table 3.5 and the effect of water stress treatments on WUE over time is shown in Fig. 3.5.

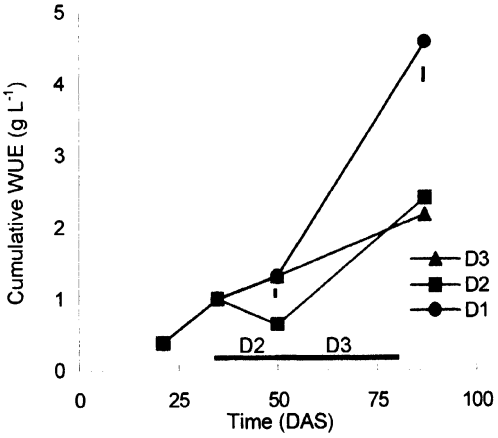


Fig.3.5 Cumulative water use efficiency (WUE) in groundnut plants exposed to different irrigation treatments. D1 – fully irrigated; D2 – early water stress; and D3 – late water stress. Vertical bars indicate SED.

Table 3.5 Cumulative ET (ml plant^{-1}) and WUE recorded at 87 DAS in fully irrigated (D1), early (D2) and late (D3) water stress treatments.

Water stress	ET (ml plant^{-1})	WUE (g L^{-1})
D1	19505	4.59
D2	20828	2.41
D3	20216	2.19
SED	12***	0.221***

Total ET in the fully irrigated treatment (D1) was 19505 ml and early (D2) and late (D3) water stress increased ET by 1323 and 711 ml, respectively (Table 3.5). In D1, cumulative WUE increased over time from 0.4 g L^{-1} at 20 DAS to 4.6 g L^{-1} at 87 DAS (Fig. 3.5). Early and late water stress reduced cumulative WUE by about 50% at 87 DAS (Table 3.5). The reduction in WUE at 50 DAS following the early water stress persisted until the final harvest. Greater cumulative ET in D2 over D1 is due an addition of excess water to bring the D2 pots to FC at 50 DAS. In addition to this, more water was added daily in D2 and D3 pots after and during the stress treatments, respectively, than in D1 pots. This was to account for excess evaporation (as the plant size was small in these pots) in order to maintain the pots at or near the pre-determined moisture content.

The values for WUE during the stress period are presented in Fig. 3.6. There is a severe decrease in WUE due to both early and late water stress treatments. During the period of early stress, WUE was 1.96 g L^{-1} in D1 while it was only 0.13 g L^{-1} in D2. During the period of late stress, WUE was 8.57 g L^{-1} in D1 and 3.17 g L^{-1} in D3, a reduction of >50%. WUE in D2, which during this period was

maintained at 100% ASM, was only 4.83 g L^{-1}, well below that of the control, D1. The higher WUE in D1 during the 50-87 d period is due to a rapid accumulation of biomass (about 75 g) during this period

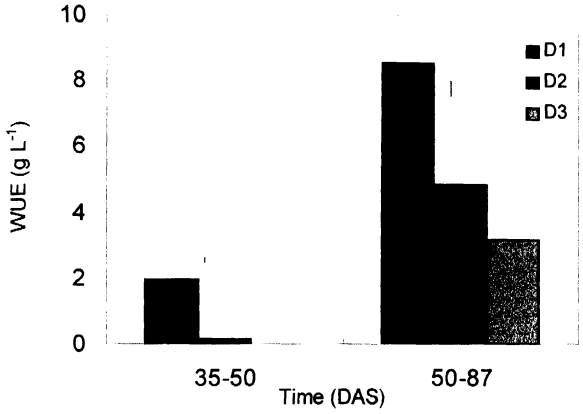


Fig. 3.6 Water use efficiency (WUE) in groundnut plants exposed to different irrigation treatments (D1 – fully irrigated; D2 – early water stress; and D3 – late water stress) during the early (D2 - 35-50 DAS) and late (D3 – 50-87 DAS) water stress periods. Vertical bars indicate SED.

3.3.4.2 Leaf number and leaf area

There were significant effects of water stress and interaction with cultivar on leaf number and leaf area at 87 DAS (Table 3.2). The total number of leaves per plant increased linearly over time in the fully-irrigated treatment from < 20 at 20 DAS to about 100 at 87 DAS (Fig. 3.7). Early water stress had a substantial effect on leaf (and branch) production and leaf senescence, and total leaf number at 50 DAS was about 50% that of D1, less than that at 35 DAS.

However, upon rewatering from 50 DAS leaf production rate increased and at 87 DAS leaf number was only about 20% less than D1. The late stress treatment also reduced leaf number significantly and at final harvest this treatment had the least number of leaves. Water stress had similar effects on plant height and node number (not presented).

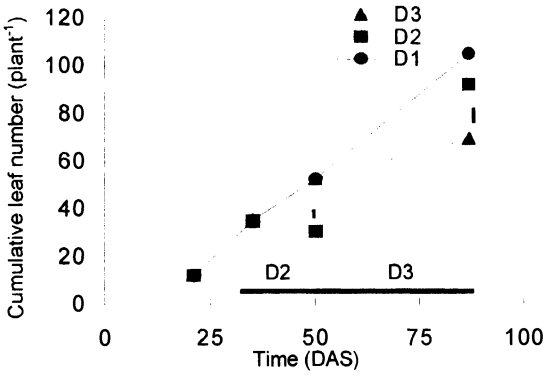


Fig. 3.7 Effect of water stress on total leaf number over time in groundnut. (D1 – fully irrigated; D2-early water stress; and D3-late water stress). Vertical bars indicate SED.

Cultivar ICG 796 was more sensitive to water stress than ICGV 86015 (Fig. 3.8). Both cultivars had similar total leaf number in D1, but water stress reduced leaf number in ICG 796 by 20 and 40% in D2 and D3, respectively, compared with reduction of <5% and 22%, respectively, in ICGV 86015. Although leaf numbers were similar in D1, leaf area in ICG 796 was significantly greater than ICGV 86015 because ICG 796 had larger leaves. The reduction in leaf area due to

early water stress (D2) was also greater in ICG 796, while in D3 both cvs had similar leaf areas.

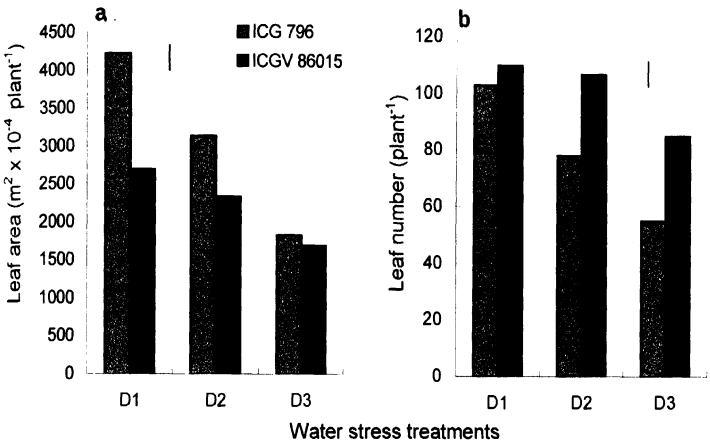


Fig. 3.8 Cultivar differences on leaf area (a) and leaf number (b) in groundnut due to water stress treatments at 87 DAS. D1-fully irrigated D2-early water stress and D3-late water stress. Vertical bar indicates SED.

3.3.4.3 Specific leaf area

Specific leaf area (SLA) is the ratio of leaf area to leaf dry weight. No interaction was observed for the SLA values between genotypes and water stress treatments in this study. Values of SLA in the water stress treatments at the end of D2 and D3 treatments are presented in Fig. 3.9. An increase in SLA values was observed during the periods when either early (D2) or late (D3) water stress treatments were imposed. In treatment D2, the SLA was 225 $cm^2\ g^{-1}$ at 50 DAS

and increased upon rewatering to 261 $cm^2 g^{-1}$ at 87 DAS. The value for SLA in the irrigated treatment (D1) was 216 $cm^2 g^{-1}$ at 50 and 87 DAS.

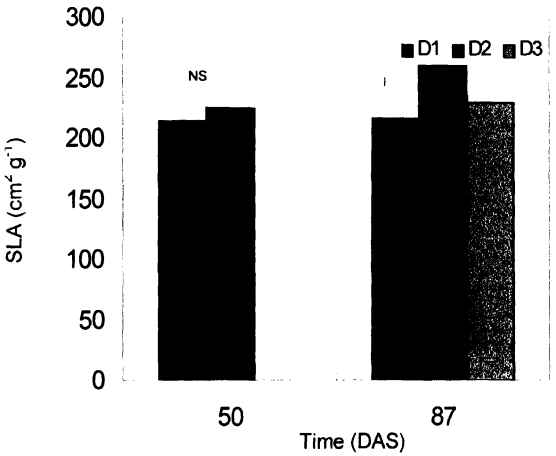


Fig. 3.9 Specific leaf area (SLA) values of groundnut plants exposed to different irrigation treatments (D1 – fully irrigated; D2 – early water stress; and D3 – late water stress) at end of early (D2 - 50 DAS) and late (D3 – 87 DAS) water stress periods. Vertical bars indicate SED where significant.

3.3.4.4 Reproductive development

Flowering in groundnut is a sensitive reproductive process and a significant water stress x cultivar interaction was recorded. The interaction was mainly associated with cultivar differences in flower production (Fig. 3.11) combined with a differential response to D2 and D3 (Fig. 3.10). Under fully irrigated conditions, ICGV 86015 produced many more flowers than ICG 796, and the rate of flower

production d^{-1} over the first 15 DAA was 5.8 and 3.5 flowers d^{-1}, respectively. The imposition of early and late water stress reduced the rate of flower production to 2.7 and 2.5 flowers d^{-1} during D2 (0 -15 DAA) and 1.3 and 0.2 flowers d^{-1} in D3 (16 - 56 DAA), respectively. These effects were relatively greater in the more profusely flowering genotype ICGV 86015.

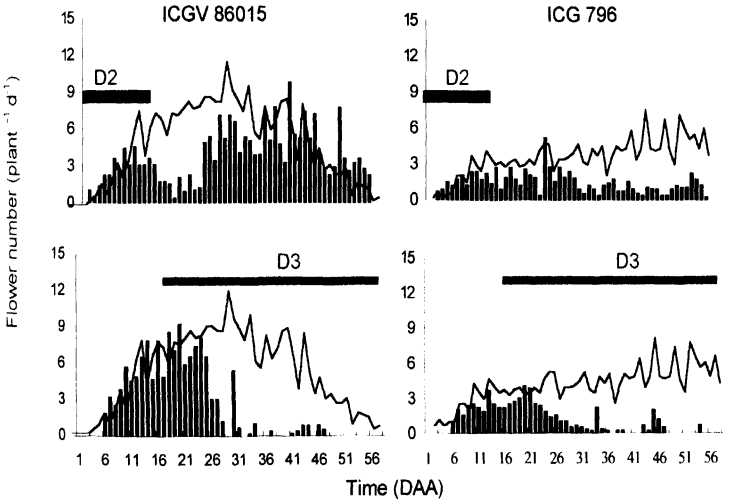


Fig 3.10 Daily flower production in groundnut genotypes subjected to early (D2) and late (D3) water stress treatments. Blue lines indicate the period of stress. Green line indicates the daily values of flower production under control conditions.

The late water stress (from 15 DAA) was unrelieved and in both genotypes flower production effectively ceased within about 10 d of starting D3. The early water stress was relieved at 15 DAA, and in ICGV 86015 flower production rapidly

recovered, though the rate was still below that in D1 over the same period. In contrast, in ICG 796 the release of water stress had little effect on flower production (Table 3.6). At final harvest, early and late water stress therefore both reduced flower number, the effect of stress being greater in D3 than D2. The relative reduction in flower number in ICGV 86015 and ICG 796 was similar, about 66 and 41, and 55 and 36%, in D2 and D3, respectively. However, because of greater flower production in ICGV 86015, the number of flowers produced in D2 and D3 were nonetheless greater or similar to ICG 796 under irrigated conditions.

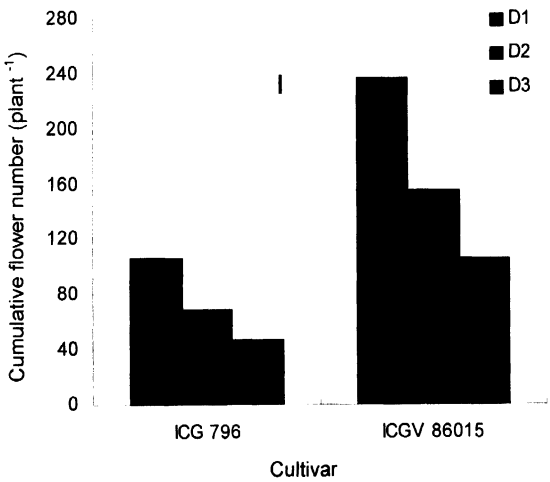


Fig. 3.11 Cumulative flower number at 87 DAS as influenced by water stress treatments (D1-fully irrigated; D2-early water stress and D3-late water stress) in groundnut genotypes ICG 796 and ICGV 86015. Vertical bar indicates SED.

Table 3.6 Effect of water stress treatments on flower production (plant $^{-1}$ d^{-1}) in groundnut genotypes ICGV 86015 and ICG 796 during the early and late water stress periods in fully irrigated (D1), early (D2) and late (D3) water stress treatments.

Water stress	Genotype	
	ICGV 86015	ICG 796
----------35-50 DAS----------		
D1	5.8	3.5
D2	2.7	2.5
SED	0.62**	
----------50-87 DAS----------		
D1	4.3	6.6
D2	4.2	0.9
D3	1.3	0.2
SED	0.42**	

3.3.4.5 Biomass and partitioning

Water stress had a significant effect on biomass and on root:shoot ratio, but not on the partitioning of biomass to pods (HI), and there were no genotype x water stress interactions for biomass, HI or root:shoot ratio.

In D1, most biomass was accumulated between 50 and 87 DAS, i.e. during the reproductive phase (Fig. 3.12). Early water stress reduced biomass from 13.8 to 10.1 g plant^{-1} at 50 DAS, and although stress was relieved at 50 DAS, final biomass was nonetheless 43% below that in D1. Late stress also reduced final biomass by 49%.

Partitioning of biomass to roots was also significantly affected by water stress. The root:shoot ratio in D1 was 0.18 and D2 reduced this slightly to 0.15. In contrast late water stress (D3) increased root:shoot ratio to 0.24.

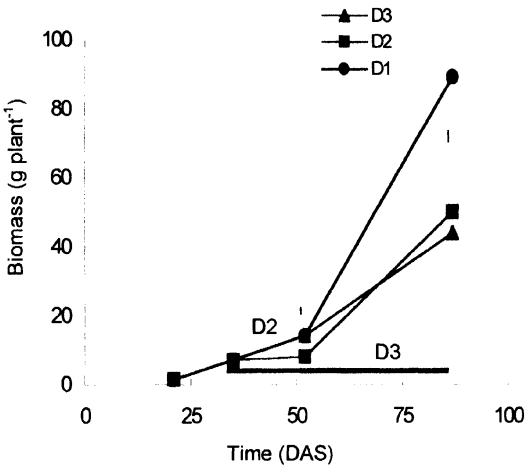


Fig. 3.12 Effect of water stress treatments on biomass (D1-irrigated, D2-early water stress and D3-late water stress). Vertical bar indicates SED.

3.3.4.6 Yield components

Although there were no genotype x water stress interactions for biomass and partitioning to pods and roots, there were genotype x water stress interactions for yield components.

The early and late water stress treatments had similar effects on flower production, pod number and pod weight when compared at the end of their respective treatment period, i.e. at 50 and 87 DAS in D2 and D3, respectively (Table 3.7). Both stresses, D2 and D3, reduced flower production, pod number and pod weight by 60 and 55, 62 and 40, 61 and 51%, respectively. However, podset in the early stress was reduced from 22 to 7%, while in late stress it was increased from 34 to 41%. By final harvest, the early stress had recovered to some extent, though values were still well below D1 values.

Table 3.7 Flower number, pod number, and pod set in irrigated (D1), early water stress (D2) and late water stress (D3) treatments as observed at 50 and 87 DAS.

Water stress	Flower number (pl^{-1})	Pod number (pl^{-1})	Pod set (%)	Pod weight ($g\ pl^{-1}$)
----------50 DAS----------				
D1	56	8	21.5	0.62
D2	23	3	6.6	0.25
SED	7.3**	1.3***	2.9***	0.145*
----------87 DAS----------				
D1	171	45	33.5	41.1
D2	113	35	34.7	23.1
D3	77	30	40.8	21.1
SED	11.5***	2.3***	4.4***	3.49***

Cultivar ICG 796 was more sensitive to early water stress than ICGV 86015 (Table 3.8). Early water stress reduced pod number by 10 and 40% in ICGV 86015 and ICG 796, respectively. Late water stress, which had a similar effect in both cultivars, reduced pod number by 40%.

Table 3.8 Interaction between water stress treatments and genotypes for pod number recorded at 87 DAS.

Water stress	ICG 796	ICGV 86015
D1	38	53
D2	22	48
D3	25	35
SED	3.24**	

3.3.5 Temperature effects and interaction with water stress

Temperature interacted significantly with early water stress in the harvest made at 50 DAS, but the interaction had disappeared by 87 DAS, and only main effects of temperature were significant at 87 DAS. Temperature treatments also had no significant interaction with cultivars, other than for pod number at 50 DAS. No significant interaction could be identified between temperature treatments and cultivars used in the study.

3.3.5.1 Water use and water use efficiency

Increase in temperature increased the amount of water lost from 35 to 50 DAS through ET, though only by 3.3% (Table 3.9). High temperature had a significant ($p<0.05$) effect on WUE during the treatment period (between 35 and 50 DAS). During the high temperature treatment, normalised WUE values were higher indicating an increase in leaf area (section 3.3.5.3) and biomass (section 3.3.5.4).

Table 3.9 Cumulative ET (ml plant^{-1}), WUE (g L^{-1}), VPD (kPa) and normalised WUE (WUE x VPD g kPa L^{-1}) recorded at 50 and 87 DAS in two temperature treatments T1and T2.

Temperature	ET	WUE	VPD	Normalised WUE
		35 - 50 DAS		
T1	3931	1.48	0.84	1.24
T2	4067	1.22	1.42	1.73
SED	1.8***	0.062*		
		50 - 87 DAS		
T1	8800	5.88	0.84	4.93
T2	8800	5.17	0.84	4.34
SED	NS	0.181*		

However in the period from 50-87 DAS, plants previously exposed to high temperature recorded significantly lower WUE compared to plants in optimum temperature. Normalised WUE during the post-high temperature period was lower (4.34 g L^{-1}) in plants previously exposed to treatment T2 (37/22°C) compared with 4.93 g L^{-1} in plants exposed continuously to T1 (28°/22°C).

3.3.5.2 Leaf area

There was a significant interaction between temperature and water stress on leaf area at 50 DAS (Fig.3.13). Early water stress (D2) reduced leaf area by 48%, whereas high temperature (T2) increased leaf area by 13%, though not significantly. However, the combination of these two stress treatments resulted in a severe and significant reduction in leaf area of 57% compared to T1D1.

The effect of this interaction had disappeared when plants reached final harvest. At 87 DAS only temperature treatments were significant ($p<0.05$) for leaf area. Plants exposed to high temperature (T2 - 37/22°C) had an area of 0.24 m^2 per plant when compared to those under ambient temperature (T1 - 28/22°C) which had a leaf area of 0.28 m^2 per plant.

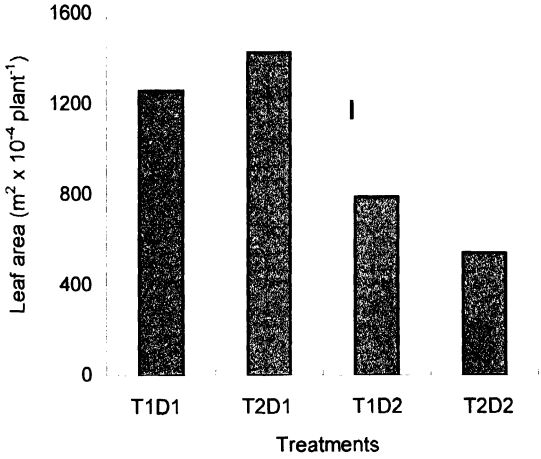


Fig. 3.13 Response of total leaf area at 50 DAS of groundnut plants exposed to both temperature (T1-28/22 and T2-37/22 °C) and water stress (D1-fully irrigated and D2-early water stress) treatments. Vertical bar indicates SED.

3.3.5.3 Reproductive development

There was no effect of high temperature, or interaction between temperature and genotype, on flower production at 50 DAS. However, high temperature did affect the total flower number produced by 87 DAS (Fig. 3.14), due to an early

cessation of flower production in T2 (Fig. 3.14a) that lowered rate of flower production (Fig. 3.14b).

The effects of high temperature were visible towards the final harvest stage (87 DAS), where a significant reduction of 20% in flower numbers was recorded due to high temperature (T2) when compared to control (T1), which had 134 flowers per plant (Table 3.10). The plants in control (T1) treatment maintained a significantly ($p<0.05$) higher rate of 3.6 flowers plant^{-1} d^{-1} until 55 DAA. The rate of flower production was reduced and finally ceased in the high temperature treatment after 40 DAA, thus high temperature treatment recorded an average rate of 2.9 flowers plant^{-1} d^{-1}.

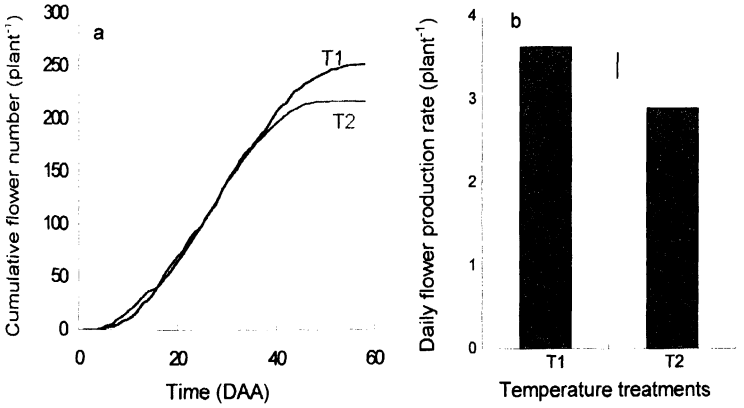


Fig. 3.14 Effect of temperature treatments (T1-28/22° and T2-40/22°C) on cumulative flower production (a) and daily flower production rate from anthesis to harvest (b).

3.3.5.4 Biomass

High temperature (T2) and early water stress (D2) treatments interacted in reducing the leaf, stem and total biomass at 50 DAS (Fig 3.15). High temperature slightly increased biomass, whereas early water stress reduced biomass. The combination of high temperature and early water stress further reduced biomass to <50% of D1. However, following relief of early water stress and high temperature stress, these interactions disappeared and at 87 DAS biomass was not significantly different in temperature treatments T1 (65 g plant^{-1}) and T2 (58 g plant^{-1}).

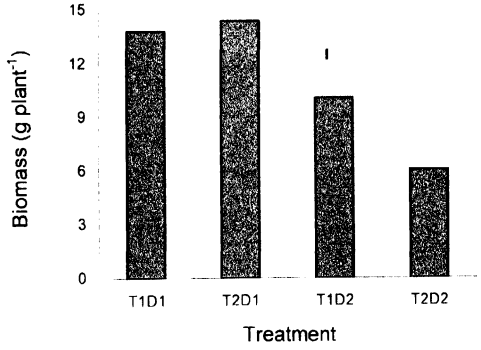


Fig. 3.15 Effect of temperature and water stress on biomass as recorded a 50 DAS.

3.3.5.5 Yield components

Although high temperature had no effect on flower number during the high temperature treatment (Fig. 3.14a), it did significantly reduce pod set, pod number and pod weight in both cultivars (Table 3.10). However, at 87 DAS high

temperature did not significantly affect pod number or weight, and there was no interaction between high temperature and cultivars either. The decrease in flower number was compensated for by a small increase in pod set.

Table 3.10 Effect of high temperature (T2 - 37/22°C) as compared to that at optimum temperature (T1 - 28/22°C) on reproductive components of groundnut observed at 50 and 87 DAS. Values for pod weight are log transformed for analysis and original values are in parenthesis.

Character	T1	T2	SED
----------50 DAS----------			
Flower number (plant^{-1})	52	51	7.26^{NS}
Pod number (plant^{-1})	7	4	1.3*
Pod weight (g plant^{-1})	-0.380(0.64)	-0.80(0.23)	0.164*
Pod set (%)	17	11	2.8*
----------87 DAS----------			
Flower number (plant^{-1})	134	107	9.4**
Pod number (plant^{-1})	37.9	35.8	1.87^{NS}
Pod weight (g plant^{-1})	1.41(29.0)	1.40(27.9)	0.047 ^{NS}
Pod set (%)	35	38	3.6 ^{NS}

3.4 DISCUSSION

Drought is a common occurrence in the SAT and is a major constraint to productivity of groundnuts. Drought is a result of water stress or water deficit and is closely associated with heat stress. The interaction between these stresses has not been investigated so far in groundnuts.

In the current study an interaction between water stress and high temperature was found for biomass only at the end of the concurrent early water stress and high temperature treatment. While high temperature increased growth and biomass, and water stress reduced biomass, the combination of the stresses exacerbated the negative effects of water stress. However, upon rewatering and/or a return to ambient temperature, these interactions disappeared and at final harvest, there was a significant effect of only water stress, but not for high temperature or interaction. These responses to water stress and temperature are summarised in Fig. 3.16 and discussed below in more detail.

The early water stress treatment (D2) was for a period of 15 d from anthesis to pod initiation, while the late water stress treatment was for a period of 35 d from pod initiation to final harvest, coinciding with phases when groundnuts are known to be sensitive to water stress (Stirling *et al.*, 1989; Chapman *et al.*, 1993d). A water stress of 60% ASM was achieved in D2, while the target moisture stress of 40% ASM was obtained in D3. Differences in intensity, duration and stage of water stress did not have any influence on the final biomass or yield recorded at

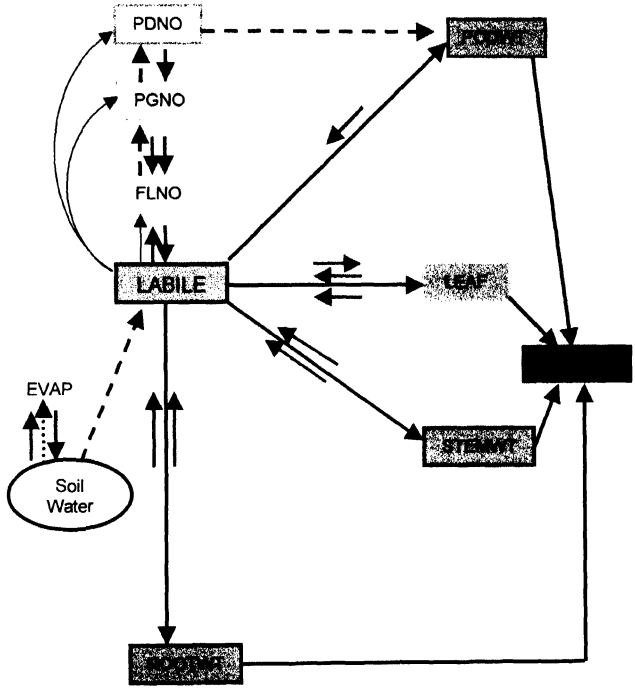


Fig. 3.16 Summary of the results of high temperature and water stress effects on growth and development of groundnut in controlled environment. (Thick black line – main route of assimilate flow; thin black line – minor route of assimilates; broken arrow = information flow; Red arrow – high temperature effects; Blue arrow – water stress effects; Red and blue arrow – interaction effect; Labile = current and stored assimilate pool; WT = weight; PDNO =pod number; PGNO = peg number; FLNO = flower number). Direction of red/blue arrows opposite to assimilate route indicates negative effects.

87 DAS. This shows that flowering period is more sensitive than pod development for water stress. Similar observations were made in studies of Reddy and Reddy (1993), when a moderate (60%) or severe (80%) depletion of available soil moisture was induced during the sensitive stages of flowering and pod development, groundnut yields were reduced by 25 to 50%.

The water stress treatments imposed in this study resulted in a decrease in WUE (total above ground biomass/total water added) of the genotypes studied. The decrease in WUE was due to a decrease in total biomass accumulated (Fig. 3.12) and only a small increase in total water added (ET). Therefore, differences in biomass were due either to differences in the proportion of ET used for transpiration (T) or soil evaporation (E_S) and/or differences in transpiration efficiency (total above ground biomass/transpiration).

Although T and transpiration efficiency (TE) were not measured directly, TE can be calculated from specific leaf area (SLA) and VPD following the procedure of Wright *et al.* (1996). Transpiration efficiency (TE), the ratio of assimilation rate (A) to stomatal conductance (g_S) can be described by the following equation:

$$TE = A / g_S = [\, p_a (1 - p_i / p_a)] / 1.6 (e_i - e_a) \ (\text{mol m}^{-2}\ \text{s}^{-1}) \qquad [3.1]$$

where A is the assimilation rate (μ mol m^{-2} s^{-1}), g_S is stomatal conductance (mol m^{-2} s^{-1}), e_i and e_a (Pa), p_i and p_a (mg L^{-1}) are the intercellular and atmosphere vapour pressure for water and CO_2, respectively. From the above relation it is apparent that decrease in p_i/p_a at a constant $e_i - e_a$ (VPD) will increase TE. Also increase in $e_i - e_a$ or VPD will decrease TE.

Wright *et al.* (1996) and Craufurd *et al.* (1999) showed that there exists a strong relation between SLA and carbon isotope discrimination (Δ – i.e. ratio of the concentration of ^{13}C to that of ^{12}C, Farquhar *et al.*, 1989). From a wide range of field environments (Wright *et al.*, 1996) and in controlled environments (Craufurd *et al.*, 1999), Δ can be predicted from SLA by:

$$\Delta = 0.03 \text{ SLA} + 14.0 \qquad [3.2]$$

Tanner and Sinclair (1983) introduced the concept that TE (g L^{-1} of water used) was inversely proportional to VPD (kPa):

$$TE = k / VPD \ (g\ L^{-1}) \qquad [3.3]$$

re-ordering the equation gives that:

$$k = TE \times VPD \ (g\ kPa\ L^{-1}) \qquad [3.4]$$

where k is the transpiration efficiency constant or nomalised TE for VPD. Wright *et al.* (1988, 1994) measured TE and VPD values from a number of experiments and then normalised TE for VPD using eq. 3.4 to obtain values of k. Wright *et al.* (1996) then regressed the values of Δ (carbon isotope discrimination) on k (Fig. 3.17), which was described by the following equation:

$$k = -0.53\ \Delta + 14.4 \quad (g\ kPa\ L^{-1}) \qquad [3.5]$$

Hence, if SLA is known the Δ values can be obtained using eq. 3.2. The Δ values so obtained can then be used to estimate k values from eq. 3.5. Finally, TE can be estimated by substituting the estimated k and measured VPD in eq. 3.3.

Values of TE were therefore calculated from above equations using SLA at 50 and 87 DAS and mean VPD from sowing to 50 and 87 DAS (Table 3.11). The calculated values of TE were in the range of 3.4 to 4.2 g L^{-1}, similar to

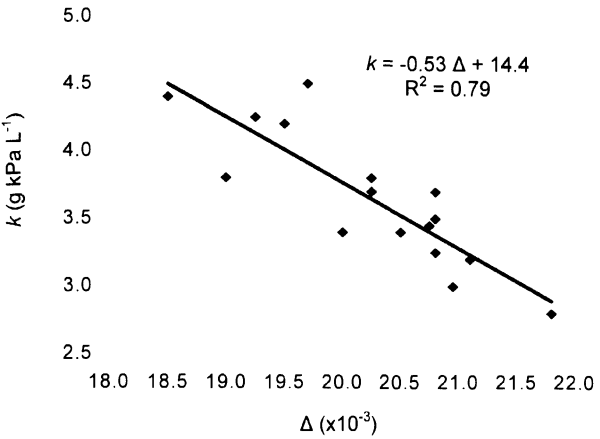


Fig. 3.17 Relationship between transpiration efficiency coefficient (*k*) and leaf carbon isotope discrimination (Δ) for data derived from groundnut transpiration efficiency studies in field based mini-lysimeters. (Source: Wright *et al.*, 1996).

Table 3.11 Observed specific leaf area (SLA) and vapour pressure deficit (VPD) in water stress treatments, and estimated values of carbon isotope discrimination (Δ), transpiration efficiency (TE), transpiration (T) from sowing to 50 DAS and sowing to 87 DAS, using the equations described by Wright *et al.* (1996).

Water stress treatment	SLA ($cm^2\ g^{-1}$)	Δ (Ratio)	*K* (g kPa L^{-1})	VPD (kPa)	TE (g L^{-1})	T (L $plant^{-1}$)
----------50 DAS----------						
D1	215	20.45	3.56	0.84	4.23	3.4
D2	225	20.75	3.40	0.84	4.05	2.0
----------87 DAS----------						
D1	216	20.48	3.55	0.84	4.22	21.2
D2	261	21.83	2.83	0.84	3.37	14.9
D3	230	20.90	3.32	0.84	3.96	11.2

other published values (Wright *et al.*, 1996 – 2.8 - 4.1 g kg^{-1}; Brown and Byrd, 1996 – 2.57 - 4.34 g kg^{-1}). Values of TE at the end of D2 (50 DAS) and D3 (87 DAS) were 4.05 and 3.96 g L^{-1}, respectively, only slightly below the value of 4.23 g L^{-1} in irrigated treatment. Therefore, TE was only slightly reduced by water stress during the stress period. Reductions in TE of up to 20% under water stress were also reported by Wright *et al.* (1994) and Mathews *et al.* (1988).

However, over the whole sowing period (i.e. from sowing to 87 DAS) TE was greatly affected by the early stress (D2) and was only 3.37 g L^{-1} compared to 4.22 g L^{-1} in D1 recorded at 87 DAS – despite the fact that both the treatments were fully irrigated between 50 and 87 DAS. Leaf area was smaller in D2, as was plant biomass at 87 DAS, suggesting that recovery from early stress was not complete. Hsiao (1973) suggested that when stressed plants are rewatered, CO_2 assimilation recovers readily but not necessarily fully. In cases where stress is not severe, full recovery was achieved in a fraction of a day, but in cases with severe stress, as in this study (60% ASM), recovery after rewatering may require one to several days.

Once TE is known, the amount of water transpired (T) could be estimated using the below given relation:

T = above ground biomass (including pods) / TE (L) [3.6]

Transpiration was very low during the first 50 d, only 3.4 L (32% of total applied) in D1, because of the small plant size and leaf area (Fig. 3.7). At 87 DAS, T was estimated to be 21.3 L, slightly higher (10%) that the total amount of water

applied (ET). This difference can be attributed to the fact that equations (3.2 to 3.6) were derived from experiments under field conditions where the VPD (>1.2 kPa) and radiation levels (~1400 μ moles m^{-2} s^{-1}) were higher than those recorded in the current study. The results also show that there was rapid increase in biomass between pod initiation and harvest, 85% of biomass was accumulated between 50 and 87 DAS. This rapid accumulation of biomass over this short period gave rise to the measured value of WUE of 8 g L^{-1}, about double that of seasonal values obtained in field experiments (Brown and Byrd, 1996; Hubick *et al.*, 1986; Wright *et al.*, 1996) and double that of estimated TE. Thus it is also possible that the mean value of TE estimated from SLA at 87 DAS is not capturing variation in TE over short time scales, and that TE was higher than 4 g L^{-1} between 50 and 87 DAS. Thus, further studies are required under controlled environments to verify the validity of this set of equations.

The final T values obtained in D2 and D3 were 30 and 50% lower, respectively, than that recorded in D1. The values show that more water was lost through E_S in the water stressed treatments as more soil was exposed to direct action of environmental factors (VPD and radiation) due to smaller canopy size. In summary, water stress had little or no effect on ET or on TE, but did greatly reduce T. Therefore, the reduction in biomass due to water stress in this experiment was due to a reduction in T. Similar reductions in biomass of about 60%, when transpiration was reduced by 60 –70%, were recorded under field conditions by Hubick *et al.* (1986) and Wright *et al.* (1996).

Plants exposed to high temperature recorded slightly higher SLA (non-significant) when compared to ambient treatment, indicating that TE was slightly increased in this treatment. This higher SLA can be attributed to larger leaf area with thinner leaves (Craufurd *et al.*, 1999) that enable the plant to dissipate heat. Although, differences for TE are small, the higher value for normalised WUE in the high temperature treatments (Table 3.9) is due to an increase in biomass during the high temperature period. This confirms that higher WUE in high temperature treatment is due to an increase in T component of ET, due to larger leaf area. This increase in leaf area is essential for the plant to meet the excess transpiration for lowering the canopy temperature (Hsaio, 1973; Black *et al.*, 1985). Patil and Patil (1993) have shown that lowered T, by with holding irrigation for a period of 4 d, increased leaf temperatures on an average by 6°C. This confirms that increased transpiration is essential to maintain leaf temperature near or lower than ambient temperature. The slight decrease in WUE during the post-high temperature period can be attributed to the disruption of the photosynthetic apparatus during the later period of 10 d high temperature treatment (Berry and Bjorkman, 1980; Bhagsari *et al.*, 1974).

Water stress reduced vegetative development, including main stem length and node number (not reported), leaf number and leaf area. Similar reductions for these parameters were reported in the literature (Lin *et al.*, 1963; Su *et al.*, 1964; Gorbert and Rhoads, 1975; Ochs and Wormer, 1959; Boote and Hammond, 1981; Nageswara Rao *et al.*, 1988, Stirling *et al.*, 1989). The rate of leaf development was slowed down in water stress treatments resulting in a lower

leaf number at both pod initiation and final harvest. This would be due to a lowered relative turgidity (Slatyer, 1955, Allen *et al.*, 1976) that inhibits cell division and expansion that are essential for leaf growth.

Water stress treatments reduced total biomass due to a reduction in both vegetative and pod weight. Similar results have been reported in many studies (e.g. Chapman *et al.*, 1993c). However, water stress did not alter the partitioning to pods (HI) and therefore pod yield varied with biomass. These results are in contrast to those obtained by Greenberg *et al.* (1992) and Chapman *et al.* (1993c), who observed significant reductions for HI in water stressed plants. This contrast in the effect on HI could be attributed to the level of stress imposed in these studies. In the current study, plants were subjected to 60% ASM in D2. In D3 plants were maintained near the pre-determined level of 40% ASM during the stress periods and plants at most only suffered a transient daily moisture stress more severe than this. In other studies water stress treatments were either more severe than 40% ASM (Chapman *et al.*, 1993c), or the duration of irrigation interval was as long as 15 d to impose a water deficit of 33% of control treatment (Greenberg *et al.*, 1992). It is well documented in other crops (e.g. maize, sorghum, pearl millet) that HI is only reduced when stress levels are severe (Muchow, 1988).

In groundnuts, flower production is synchronised with leaf production once flowering is initiated. The flowers appear at the axils of the cataphylls or foliage leaves. The reproductive and vegetative axes appear to emerge from the same

node (Norden, 1980). Due to reduced branching and leaf number, flower production was also slowed down under water stress periods, resulting in lower flower number at 50 and 87 DAS, respectively. Harris *et al.* (1988) made similar observations for leaf and flower production in groundnuts.

A reduction in flower number early in the cycle reduces the potential number of pegs and pods. Water stress also reduced the percentage of pegs and pods set. This effect on fruit-set was greater than the effect on flower number. Hence, other factors than just reduction in flower number are responsible for reduced peg and pod number under water stress. A slower accumulation of assimilates under water stress, due to delayed leaf development, further reduced total number of pegs or pods formed (Williams *et al.*, 1986; Nageswara Rao *et al.*, 1988; 1989; Wright *et al.*, 1991). The reduction in peg and pod number can be related to impaired pollination under water stress conditions during flowering (Jain *et al.*, 1997). This decrease in peg and pod number could also be due to anther abnormalities as observed in wheat (Sheoren and Saini, 1996) and/or due to ovule abnormality under water stress as observed in maize (Moss and Downey, 1961).

Greater the number of flowers produced during the first two weeks after anthesis, greater is the number of pods produced (Sastry *et al.*, 1985). Thus, the earlier plants establish their potential sink the greater will be the pod yield. It was observed in groundnut that only 20% of flowers under optimum conditions (Donovan, 1963, Ono, 1979), and sometimes less than 15% (Lim and Hamdan,

1984), produce pods. In the late stress flowering was halted 10 d after imposition of stress and only the flowers produced early resulted in final pod yield. Plants exposed to early stress flowered on rewatering, and an increase in peg and pod set was recorded. This did not add to the final pod yield as most of the pegs formed did not reach the soil or those that reached the soil could not mature into full pods to add to final yield by 87 DAS. Similar observations were made in other studies on peg elongation and peg conversion to pods (Chapman *et al.*, 1993a; Harris *et al.*, 1988).

Unlike early or late water stress, no reduction in flower number occurred due to high temperatures (37/22 °C) imposed for 10 d, starting at anthesis, but a decrease in peg and pod number was observed in the harvest made at 50 DAS. There was no reduction in leaf number or branch number under high temperature conditions at 50 DAS. Hence, the sites for flower production are not limiting which was not the case in water stress treatments. Previous studies by Ong (1984), Ketring (1984) and Vara Prasad *et al.* (1999a) have shown that under high temperatures (>34°C) peg and pod numbers were reduced by 33-50%. Similar reductions were observed in the present study. A reduction in peg and pod numbers would also result from damaged pollen mother cells (Warrag and Hall, 1984), poor pollen viability (Halterlien, 1979; Halterlien *et al.*, 1980; De Beer, 1963), impaired style and ovule function (Gross and Kigel, 1994) or failure of fertilisation (Ormrod *et al.*, 1967). These effects are examined in more detail in Chapter 4 and 5. This decrease in peg and pod number lowered the pod weights by 63%.

Despite a decrease in flower numbers, no differences for pod weight could be observed at final harvest between temperature treatments. This decrease in flower number could be a result of damage to reproductive primordia during the high temperature period as reported by Vara Prasad *et al.* (1999a). Fortanier (1957) recorded similar decrease in flower number at later stages (80 DAS) of crop growth. However, no difference in pod weights at final harvest could be observed as flower reduction occurred after heat stress and flowers formed late in the crop growth do not contribute to final yield.

High temperature did not significantly affect the number or weight of vegetative components in the harvest made at 50 DAS, at the end of the treatment. In the harvest made at 87 DAS, a significant decrease in leaf area and leaf weight was recorded. Ketring (1984) recorded similar delay in the effect of high temperatures on leaf area and weight. When high temperature of 35°C was started at 21 DAS, reduction in leaf area and leaf weight was recorded only at 63 DAS. This delay in damage or lack of instantaneous effect could be attributed to the greater heat killing time required for groundnut tissue membranes when compared to crops like soyabean, chickpea and pigeonpea (Srinivasan *et al.*, 1996). A decrease in stem weight was also observed under high temperature conditions, which was visible at final harvest. This is an indication of movement of stored assimilates to source survival (leaves) or sink (pod) development under stressed periods. Poorter and Nagel (2000) made similar observations in their review of environmental effects on biomass allocation in cereal crops.

Interaction between temperature and water stress was found to be negative for vegetative components. High temperature increases vegetative components and water stress decreases these same components. The increase in vegetative weight could be attributed to higher optimum temperature of the photosynthetic process compared to the optimum of 28°C for vegetative and reproductive growth (Boote *et al.*, 1999). Studies in identifying the tolerance of this process is essential in groundnut, as around 48-49°C was required for inactivation of photosynthesis in *Tridestromia oblongifolia* (Bjorkman *et al.*, 1980). Talwar *et al.* (1999) in their study with three genotypes, ICG 1236, ICGS 44 and ICG 476, observed genotypic differences for photosynthetic rates. ICG 1236 and ICGS 44 recorded 28.7 and 18.7 mmol m^{-2} s^{-1}, respectively, at 35°/30°C (day/night), compared to 16.5 and 18.9 mmol m^{-2} s^{-1}, respectively, at 25°/25°C. Further studies to confirm temperature tolerance of photosynthesis that would lead to incorporating this character into genotypes for areas with hot climates are required.

A combined effect of stresses, water stress and high temperature, further decreased vegetative components that were reduced due to water stress. This combination of stress treatments would have raised the leaf temperatures to above critical for processes like photosynthesis and membrane thermostability, thus causing a severe decrease in assimilate production and in turn vegetative weight. Similarly, Paulsen (1994) reported a marked interaction between high temperature and water stress, which combine to exacerbate injury to photosynthesis in wheat. High temperature aggravates drought injury by reducing

photosynthesis and preventing plants from adjusting osmotically to stress. These interactions were significant only at 52 DAS in the present study. But, they disappeared as plants reached 87 DAS, indicating the plasticity of groundnut plants to recover from stress treatments.

Observations for increased severity of water stress under high temperatures could not be recorded for peg or pod number or pod weight. No interaction was observed for reproductive weights. Pod filling starts 15 d after flowering, combined stress was withdrawn before the initiation of pod filling and hence provided unstressed period for pod and seed development. Observations conform to those made by Nicolas *et al.* (1984) that a decrease in grain yield occurs only when heat stress and water stress are combined during the grain filling period.

Cultivars interacted and reacted differently to water stress but not to high temperature. Greater reductions for leaf weight and stem weight were found in ICG 796 than in ICGV 86015 under similar water stress conditions. These effects are mainly due to differences in cultivar ability to establish vegetative or reproductive components during ontogeny. ICG 796 established greater biomass and hence greater reductions for these components occurred when compared to ICGV 86015. Greater decrease in ICG 796 can be attributed to use of stored assimilates for maintenance processes (e.g. respiration) for a greater plant size. Such genotypic differences to water stress in groundnut are widely reported in literature (Williams *et al.* 1986; Chapman *et al.*, 1993a),

Under similar levels of water stress ICGV 86015 is superior to ICG 796 due to faster and larger flower and pod number established by the genotype, but no significant differences in reproductive dry weights was evident. This is due to significantly greater number of immature pods in ICGV 86015 than in ICG 796 (data not shown). These immature pods had smaller seeds and thus reduced reproductive yield in ICGV 86015. Presence of higher number of developing pegs and pods created intra-sink competition for available assimilates (Chapman *et al.*, 1993a) and thus prevented effective pod formation in ICGV 86015. The lack of differences for pod weights could also be due to the fact that the plants were harvested before reaching maturity.

3.5 CONCLUSIONS

It is evident from this study that water stress either independently or in combination with high temperature affects growth and development of groundnuts. Water stress reduces groundnut yield by reducing vegetative plant growth. Water stress also reduces reproductive weight by reducing flower number and hence pod number that are visible at final harvest. In contrast, high temperature severely disrupts reproductive processes. High temperature decreases peg and pod number by disrupting pollen viability and pollination instantaneously in flowers. A combination of these two stresses further aggravates reductions in groundnut biomass components, mainly by reducing vegetative components, i.e. source, and by decreasing potential sink establishment. Thus, tolerance to both water stress and high temperature is essential to improve groundnut yields of SAT.

MEMBRANE THERMOSTABILITY AND THE RESPONSE TO TEMPERATURE OF POLLEN GERMINATION AND POLLEN TUBE GROWTH IN GROUNDNUT

4.1 Introduction

High temperature studies conducted so far in groundnuts have shown that temperatures >34°C during the reproductive period severely reduce both peg and pod number (Ketring, 1984; Wheeler *et al.*, 1997; Vara Prasad *et al.*, 1999a, 1999b, 2000a). Temperatures >36°C during the first 6 h of the day (morning) severely reduced peg and pod number; whereas high temperature during afternoon had no effect on peg or pod set (Vara Prasad *et al.*, 2000a). This reduction in peg and pod number has been attributed to fewer pollen grains and poorer pollen viability (Vara Prasad *et al.*, 1999b). It has also been established that a single day of heat stress during the most sensitive stages of flower development - microsporogenesis and anthesis - is sufficient to reduce groundnut pod numbers significantly (Vara Prasad *et al.*, 2001).

Fruit set is reduced by high temperature [e.g. 35/23°C in tomatoes (Baki and Stommel, 1995; Peet and Bartholomew, 1996); 32/27°C in common bean (Gross and Kigel, 1994) and 30/20°C in wheat (Saini *et al.*, 1983)] in many crops due to a decrease in pollen viability and germination, and the disruption of pollen tube growth. Genotypic differences in response to temperature have also been identified for pollen germination and pollen tube growth, and in tomato high temperature tolerant genotypes have been identified (Rudich *et al.*, 1977; Shelby *et al.*, 1978; Ahmadi and Stevens, 1979; Weaver and Timm, 1989; Dane *et al.*, 1991).

Response to temperature of pollen germination and pollen tube growth has not been examined in groundnut. However, the structure and development of pollen (Willcox *et al.*, 1990, Xi, 1991), pollen production (Trivedi and Verma, 1975), temperature requirements for viability and germination (Oakes, 1958; De Beer, 1963), and *in vitro* germination and growth (Faucetti and Emery, 1974; Niles and Quesenberry, 1992) have been studied. Lim and Gumpil (1984) concluded that pollen dehiscence and pollination occur around 7:00-8:00 AM and fertilisation takes place at midday. Oakes (1958) recorded that temperatures >36°C are lethal for pollen germination and pollen tube growth.

Membrane thermostability is another important technique that has been widely used in different crops, such as, soyabean (Martineau *et al.*, 1979; Srinivasan *et al.*, 1996); chickpea and pigeonpea (Srinivasan *et al.*, 1996); and cowpea (Ismail and Hall, 1999), to classify genotypic tolerance to temperature. Studies have also been conducted in groundnuts to identify heat tolerance based on membrane thermostability (Ketring, 1985; Srinivasan *et al.*, 1996; Chauhan and Senboku, 1997; Talwar *et al.*, 1999). Membrane dysfunction is a physiological process disturbed most by heat stress (Levitt, 1980; Quinn, 1989). It results in increased permeability and leakage of electrolytes, which, in turn, reduces photosynthetic or mitochondrial activity, and the ability of plasmalemma to retain solutes and water (Lin *et al.*, 1985). Membrane thermostability indicates the general heat tolerance of a crop species or genotype; whether this general tolerance is associated with tolerance of specific processes like pollen germination or pollen tube growth has not been yet established.

The evaluation of genotypes in the field for high temperature tolerance is not straight forward, as facilities capable of controlling temperature over a large area are required (e.g. Morfo and Hall, 1992). If natural hot environments are used, confounding between environmental variables cannot be easily avoided. Techniques like *in vitro* pollen germination and pollen tube growth can be used to screen many genotypes quickly and economically for high temperature tolerance. The main objective of this study was to investigate the capacity for pollen germination and pollen tube growth *in vitro* among groundnut cultivars in response to a range of controlled temperatures; and hence to identify heat tolerant genotypes.

4.2 Materials and Methods

4.2.1 Experimental material

Groundnut plants of twenty-one genotypes were grown in a poly-tunnel facility at the Plant Environment Laboratory, The University of Reading, Reading, UK. These genotypes were selected based on their known varying tolerance to water stress and temperature (Table 4.1). Pre-germinated seeds were sown in 15 cm high by 10 cm diameter pots containing a soilless mixture of sand, gravel, vermiculite and loamless peat compost mixed in proportions of 4:2:2:1, by volume, respectively. A commercial controlled-release fertiliser (0.15 kg kg^{-1} N, 0.10 kg kg^{-1} P, 0.12 kg kg^{-1} K, 0.02 g kg^{-1} MgO plus trace elements; Osmocote Plus, Scotts UK Ltd, UK) was incorporated into the mixture at the manufacture's recommended rate of 5 g L^{-1}. Seeds were not inoculated with rhizobia and so plants were dependent on inorganic nitrogen. All pots were soaked and drained

for 24 h before seedlings were planted; thereafter they were hand-watered. Plants were grown continuously at 28/22°C (day/night) with a 12 h photoperiod.

4.2.2 Membrane thermostability

Membrane thermostability was determined following the procedure described by Srinivasan *et al.* (1996). The top 3rd or 4th tetra-foliate leaf from plants grown under optimum temperature regime of 28°/22°C (day/night) was picked at flowering. Six sets of 10 leaf discs of 2 cm diameter were cut from the leaflets using a cork borer. Each set of 10 leaf discs was used as a replicate. Three replications were used for each temperature treatment. The leaf discs were washed three to four times in deionised water to remove electrolytes from injured cells at the cut edge and any surface adhering electrolytes. Sets of 10 leaf discs were immersed in 30 ml of water (at 25°C) in test tubes and were then subjected to a temperature stress of 54°C for 15 min in a water bath. The control tubes were maintained at 25°C. A temperature of 54°C was identified by Srinivasan *et al.* (1996) as the optimum heat killing temperature in groundnut. After cooling to room temperature, samples were incubated at 10°C for 16 h and conductivity was measured with a conductivity meter (Fisher Scientific, Pittsburgh, USA). The tubes were then covered with aluminum foil and autoclaved at 120°C for 15 min to release all electrolytes. After cooling to 25°C, the contents were mixed and final conductance was measured. The injury (RI) was determined as follows:

$$RI\ (\%) = 100 - \{1-[1-(T_1/T_2)]/[1-(C_1/C_2)]\} * 100 \qquad [4.1]$$

Table 4.1 Pedigree, origin, ecotype, and known tolerance to water stress and high temperature, of the 21 groundnut genotypes used in the study.

Genotype	Pedigree	Origin	Ecotype†	Tolerance$		
				Water stress	High temperature	Membrane thermostability
ICG 1236(Ah 6179)	-¶	India	SB	T	T	T
ICGV 86015	ICGS44 x TG 2E	India	SB	S	MT	MS
ICGV 92109	ICGV 87399 x Ah 7827	India	VB	S	-	MS
ICGV 92113	ICG 1697 x ICG 4790	India	SB	S	-	S
ICGV 92116	(TMV 10 X CHICO) X ICGV 86742	India	VB	S	-	S
ICGV 92118	ICGV 87340 X ICGS 11	India	SB	S	-	S
ICGV 92120	ICG 3736 X (TMV 10 X CHICO)	India	VB	-	-	MS
ICGV 92121	Ah 7827 X ICGS 11	India	VB	-	-	S
ICGV 93232	ICGV 87399 X Ah 7827	India	VB	S	-	MS
ICGV 93233	ICGV 87399 X Ah 7827	India	VB	S	-	MS
ICGV 93255	ICGS 30 X ICGS 11	India	SB	-	-	S
ICGV 93260	ICGS 11 X ICG 4728	India	SB	-	-	S
ICGV 93261	ICGS 11 X ICG 4728	India	SB	-	-	MS
ICGV 93269	ICGS 11 X JL 24	India	SB	-	-	MS
ICGV 93277	ICGV 87399 X Ah 7827	India	SB	-	-	MS
47-16 (ICG 2904)	-	India	SB	S	MT	MT
55-437 (ICG 8242)	Selection from a population	Argentina	SB	T	T	T
ICGS11	Selection Robut 33-1-18-8	India	SB	T	MT	MT
Kadiri-3	Robut 33-1	India	SB	T	S	MT
TMV2	Selection from Gudianthum bunch	India	SB	T	MT	MT
TS32-1	Selection following hybridisation, Spantex Te. 3	Tanzania	SB	T	MT	MT

(† SB = Spanish bunch; VB = Virginia bunch; $ T = tolerant; MT = moderately tolerant; MS = moderately susceptible; S = susceptible¶ = no information available)

where T and C refer to the conductance in treatment and control tubes, and subscripts 1 and 2 refer to readings before and after autoclaving, respectively. The conductance in treatment tubes is a measure of electrolytes leaked from cells due to the degree of injury to membranes. The control gives the measure of leakage due solely to the cutting and incubation of leaf discs.

4.2.3 Pollen collection

Flowers were collected from each genotype (7-8 days after flower initiation) at the time of anther dehiscence, between 0700 and 0800 h (Lim and Gumpil, 1984), and were placed in petri-dishes lined with moistened filter paper to avoid pollen desiccation. Pollen was extracted either by pressing the keel petal or by removing pollen from the anthers using a needle. Pollen from 10 flowers was put on a slide and mixed thoroughly using a nylon hair brush. Pollen was then transferred, within half an hour of picking the flowers, on to the growth medium.

4.2.4 Growth media

The germinating media consisted of 100 g kg^{-1} sucrose, 100 mg kg^{-1} H_3BO_3, 250 mg kg^{-1} $Ca(NO_3)_2$, 200 mg kg^{-1} $MgSO_4$ and 100 mg kg^{-1} KNO_3 in deionised water (Niles and Quesenberry, 1992). The media was solidified with 2% Agar. Pollen germination and tube growth were determined by placing 2 ml of germinating media on a glass slide and inoculating it with a sample of pollen. Slides with media and pollen were placed in petri-dishes lined with moist filter paper thus serving as germination chambers. By gently tapping the nylon hair brush loaded

with pollen grains, an even spread of pollen on the surface of the growth medium was achieved.

4.2.5 Temperature treatments

Petri-dishes containing pollen of each genotype were exposed to different temperatures ranging from 10° to 45°C at 2.5°C intervals in incubators. Temperature of the medium in the incubators was measured using copper-constantan micro-thermocouples. The temperatures were logged at 10s interval and averaged every 10 min. The temperature averaged during the period of germination was used for calculating the response to temperature.

4.2.6 *In-vitro* pollen germination

A pollen grain was considered to have germinated when the germinated pollen tube length was equal or more than the diameter of pollen. Pollen was allowed to germinate for 45 min before any counts were made. Counts were made at random in three fields under a low power, 6.5x, microscope (Nikon Scientific, Japan). Each field was considered as a replicate for statistical analysis. Around 1500 pollen grains were used for determining the germination percentage. Germinated pollen was counted until no further pollen germination was observed. Germination percentage was calculated using equation 4.2:

$$\text{Germination (\%)} = \frac{\text{number of germinated pollen per field}}{\text{total number of pollen per field}} \text{X100} \qquad [4.2]$$

4.2.7 *In-vitro* pollen tube growth

The *in-vitro* elongation of pollen tubes was measured on germinated pollen grain. Pollen tube length was measured at 45 min intervals. An ocular micrometer was used to measure pollen tube length under a high power, 40x, microscope (Fisher Scientific, Pittsburgh, USA). In each temperature treatment, three sets, each of 15 pollen tubes, were considered as three replicates. Length of 15 pollen tubes was measured at each observation time and was averaged. Measurements were made until 4 h after germination, beyond which no increase in pollen tube length was recorded. Observations made at different temperatures were used to fit response of pollen tube length to temperature.

4.2.8 Statistical analysis

Values obtained for membrane thermostability (RI %) were analysed using the ANOVA procedure in GENSTAT 5 (GENSTAT 5 Committee, 1997) with three replications (Srinivasan *et al.*, 1996).

Percentage germination and pollen tube length were analysed using linear and non-linear regression techniques (Fig. 4.1). The best fit of a regression equation was identified for response of germination percentage and pollen tube length to temperature based on the amount of variation the fit accounted for. Quadratic (Yan and Wallace, 1996, 1998), cubic or higher order polynomial (Tollenaar *et al.*, 1979), beta distribution model (Yin *et al.*, 1995), bi-linear/broken stick (Omanga *et al.*, 1995, 1996; Craufurd *et al.*, 1998) and modified bi-linear (Omanga, 1994) equations were tested for goodness of fit.

When temperature transgresses the optimum temperature, the use of bilinear model may not always be meaningful. Craufurd *et al.* (1998) point out that the estimation of T_{min} (or T_b) usually requires considerable extrapolation and the standard error (s.e.) of this T_{min} is large in comparison with the s.e. of optimum temperature (T_{opt}). Further, the maximum rate of any process at T_{opt} is likely to be over estimated since it is obtained from two linear equations, while the real response curve is generally somewhat smooth. To overcome this, equation 4.3 described below (Omanga, 1994) can be used to study the response across a range of temperatures, where

$$\text{Pollen germination (\%) or pollen tube length} = a + b1(T-T_{opt}) + b2\ ABS\ (T-T_{opt}) \qquad [4.3]$$

where T_{opt} = the optimum temperature to be estimated; T= the temperature at which pollen germination or pollen tube length was recorded; a = maximum rate of germination where T = T_{opt}; $b1$ and $b2$ = parameters combined to determine the sensitivity to the mean temperature both below and above T_{opt}; *ABS* = absolute values of $T-T_{opt}$. Values of minimum (T_{min}) and maximum (T_{max}) temperatures for each genotype were calculated by using the following equations 4.4 and 4.5.

$$T_{min} = \frac{a + (b2 - b1) * T_{opt}}{b1 - b2} \qquad [4.4]$$

$$T_{max} = \frac{a - (b2 + b1) * T_{opt}}{b1 + b2} \qquad [4.5]$$

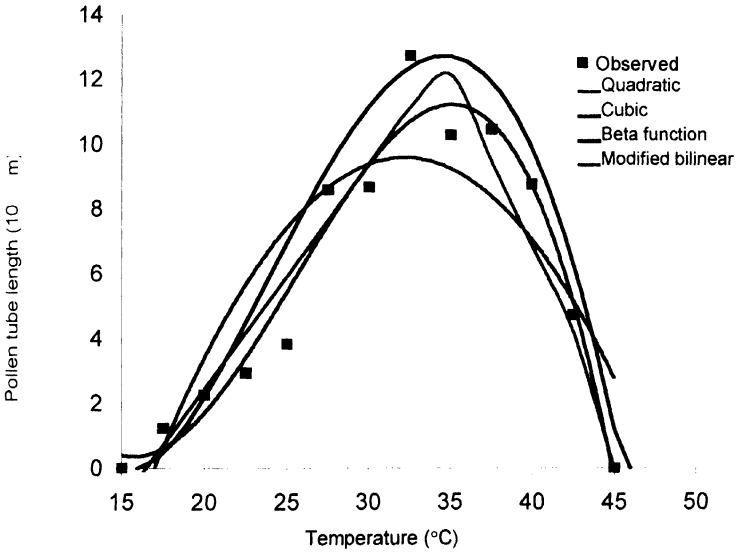


Fig. 4.1 Comparison of fitted equations for pollen tube length response to temperature between 10 °C and 47.5°C in groundnut genotype ICG 1236.

This modified bi-liner equation gives a smooth fit to the temperature response and reduces the over estimation of the minimum, optimum and maximum temperatures for a given process.

Equation 3 can be easily fitted to the experimental data using the PROCNONLIN procedure in SAS 6.2 (SAS Institute) or through the non-linear regression procedure in GENSTAT 5. The Newton-Gauss Maximum Likelihood program in GENSTAT 5 has been used for this purpose. GENSTAT 5 uses an iterative process to determine the T_{opt} based on the least root mean squared deviation value between observed and predicted values. Values of maximum pollen germination and maximum pollen tube length obtained after 225 min in each field or replication of different temperature treatments were used to fit the modified bi-linear equation. The values of T_{min}, T_{opt}, T_{max}, for maximum germination and pollen tube length for each replicate were analysed using ANOVA of GENSTAT 5 to identify the genotypic differences.

Pollen tube growth rate in response to temperature was also studied. The time to reach 50% of maximum length was calculated as the time at which length ≥ 0.5 x length at 225 min, as shown in equation 4.6:

$$t_{1/2} = (\log_e((L_{1/2}-A)/B)) / (\log_e R) \qquad [4.6]$$

where A, B and R are the estimates of intercept, slope and constant, respectively from the exponential fit (eq. 4.7) to the pollen tube length values across time at different temperatures:

$$Y = A + B \times R^{t} \quad [4.7]$$

The inverse of $t_{1/2}$, the rate of tube growth, was then plotted against temperature and linear regression fitted. The linear model (eq. 4.8) obtained for each of the genotypes was used to calculate the base temperature (T_b) where:

$$1/t_{1/2} = a + bt \quad [4.8]$$

$$T_b = -a/b \quad [4.9]$$

Principal component analysis (PCA) for pollen germination and pollen tube growth parameters was carried out using GENSTAT 5 to identify heat tolerant genotypes. Values of reduction in pollen germination (RGER) and pollen tube length (RPTL) at 40°C over that at optimum temperature, cardinal temperatures (T_{min}, T_{opt} and T_{max}) obtained from modified bi-linear fit, RI values, and reciprocal of time to reach 50% of maximum pollen tube length ($1/t_{1/2}$ PTL) obtained in this study for each genotype were used in PCA analysis.

4.3 Results

4.3.1 Membrane thermostability

There were clear differences among groundnut genotypes in RI when subjected to 54 °C for 15 min (Table 4.2). The mean value of RI was 22% and most genotypes were significantly higher or lower from this value.

Table 4.2 Percentage relative injury (RI) of 21 groundnut genotypes.

Genotype	RI (%)
ICG 1236	45
ICGV 86015	15
ICGV92109	16
ICGV92113	7
ICGV 92116	7
ICGV 92118	6
ICGV 92120	8
ICGV 92121	5
ICGV 93232	10
ICGV 93233	32
ICGV 93255	8
ICGV 93260	9
ICGV 93261	17
ICGV 93269	20
ICGV 93277	11
47-16	40
55-437	52
ICGS11	35
Kadiri-3	31
TMV2	30
TS32-1	21
Mean	22
SED ($p<0.001$)	6.1

Genotypes ICG 1236 and 55-437 showed less injury with high RI values of 52 and 45%, respectively, and were therefore the most thermotolerant. Moderate injury was observed in genotypes 47-16, ICGS 11, Kadiri 3, TMV 2 and ICGV 93233, with values between 30 and 40%. The rest of the genotypes had very high injury with RI values around or less than 20%, of these ICGV 92121 and ICGV 92118 were most injured, with values of 5 and 6%, respectively.

4.3.2 Pollen germination

Pollen germinated quickly and reached their maximum percentage germination within 60 min of their contact with the agar medium. The observed values for germination and their modified bi-linear fits are shown in Fig. 4.2. The model parameters describing the fit with their R^2 values are shown in Table 4.3. Genotypes significantly differed in their maximum percentage of germination (Table 4.4), which ranged from 35.7% in ICGV 93269 to 76.3% in ICGV 93233, with a mean germination of 56%.

Genotypes differed significantly in their T_{min}, T_{opt} and T_{max}, obtained from the modified bi-linear fit (Table 4.4). Minimum temperature for pollen germination averaged 14.0 ±2.5°C. Among the genotypes studied, pollen of four genotypes (e.g. ICGV 92118) initiated germination at temperatures of <12°C while in TS 32-1 a temperature of 16.6°C was required. Pollen germination reached a maximum at T_{opt}, which was specific to each genotype. Optimum temperature ranged from 25.5° to 35.0°C, with a mean of 30°C. Genotypes ICG 1236, TMV 2, TS 32-1 and ICGS 11 had high values of T_{opt} >33°C.

Maximum temperature (T_{max}) or lethal temperature beyond which no germination occurred in the *in vitro* medium averaged to 43.4 ±3.8°C (Table 4.4). The most sensitive genotypes were Kadiri 3 and ICGV 92116, which recorded a maximum temperature of only 36.7° and 38.6°C, respectively, at which no pollen germination was observed. All genotypes that had high values for T_{opt} also had correspondingly higher values for T_{max}. No significant correlation could be recorded for T_{min} versus T_{opt} or T_{max}. A slightly higher correlation (r=0.29) was recorded between T_{opt} and T_{max}.

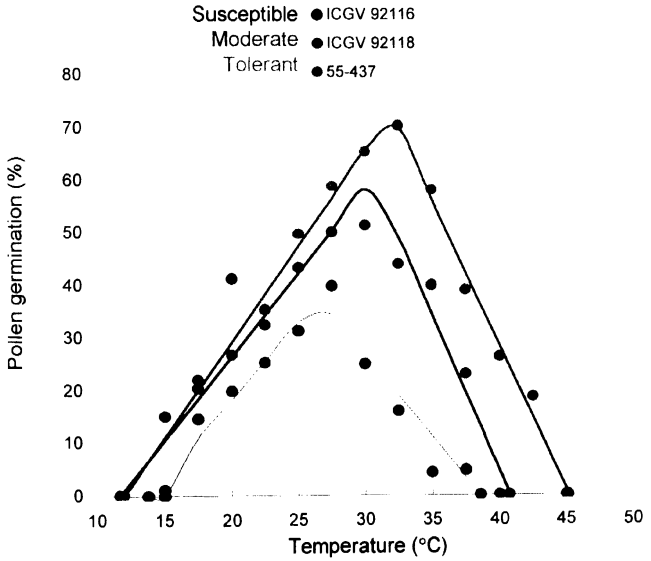


Fig. 4.2 Effect of temperature on percentage pollen germination of susceptible (T_{opt} < mean-LSD), moderately tolerant (T_{opt} = mean±LSD) and tolerant (T_{opt} > mean+LSD) genotypes. Symbols are observed values and lines are fitted values.

Table 4.3 Model parameters from Newton-Gauss Maximum Likelihood Program in GENSTAT 5 describing pollen germination response to temperatures between 10 °C and 47.5 °C.

Genotype	*a* ± s.e	*b*1 ± s.e.	*b*2†	T_{opt}±s.e.	R^2 (n)
ICG 1236	52.4±2.04	-1.42±0.251	-4.02	34.4±0.51	95.7 (9)
ICGV 86015	77.4±2.89	+0.33±0.315	-5.01	29.4±0.58	95.5 (9)
ICGV 92109	45.9±2.88	-0.51±0.325	-3.63	29.6±0.79	91.5 (8)
ICGV 92113	42.4±1.72	+0.71±0.123	-2.82	25.5±0.63	89.2 (8)
ICGV 92116	37.4±2.89	-0.09±0.355	-3.02	26.5±0.97	87.5 (7)
ICGV 92118	60.1±4.45	-0.71±0.715	-4.23	30.6±1.07	85.1 (8)
ICGV 92120	44.3±2.53	-0.03+0.328	-2.95	28.2+0.98	89.3 (9)
ICGV 92121	65.5±4.74	-0.42+0.595	-4.41	31.1±1.03	85.6 (9)
ICGV 93232	69.6±3.05	-1.15±0.494	-5.09	32.0±0.64	94.3 (8)
ICGV 93233	78.4±3.75	+0.24±0.393	-4.83	30.9±0.76	93.4(10)
ICGV 93255	54.7±1.74	+0.48±0.188	-3.77	28.0±0.45	97.1 (9)
ICGV 93260	53.2±2.92	+1.01±0.355	-3.23	26.1±0.75	92.0 (9)
ICGV 93261	48.9±2.78	-0.43±0.302	-3.45	31.5±0.79	91.7 (9)
ICGV 93269	35.7±1.78	-0.18±0.222	-2.61	28.4±0.69	93.7 (8)
ICGV 93277	61.9±3.88	+0.19±0.385	-4.11	28.8±0.95	89.4 (10)
47-16	53.6±5.97	-0.12±0.542	-3.98	28.9±1.52	75.8 (9)
55-437	72.7±2.37	-0.93±0.247	-4.57	31.9±0.50	96.6 (10)
ICGS 11	52.0±2.04	-1.53±0.247	-3.98	35.0±0.51	95.6 (9)
K3	39.4±1.71	-0.58±0.231	-3.83	26.3±0.42	85.1 (8)
TMV 2	68.9±2.32	-2.04±0.285	-5.25	34.8±0.43	97.0 (10)
TS 32-1	66.8±3.71	- 2.46±0.595	-6.21	34.4±0.62	93.0 (8)

† b1 and b2 have same s.e. values.

Table 4.4 Maximum germination, and three cardinal temperatures (from bi-linear fit) for *in vitro* pollen germination of groundnut.

Genotype	Maximum germination (%)	T_{min}	T_{opt}	T_{max}
ICG 1236	52.0	14.3	34.4	44.1
ICGV 86015	72.7	14.9	29.4	45.9
ICGV 92109	51.3	14.9	29.6	40.7
ICGV 92113	46.7	13.4	25.5	43.7
ICGV 92116	40.0	13.8	26.5	38.6
ICGV 92118	51.3	11.7	30.6	40.7
ICGV 92120	42.0	11.9	28.2	41.9
ICGV 92121	55.0	11.8	31.1	41.9
ICGV 93232	65.3	13.7	32.0	42.7
ICGV 93233	76.3	14.2	30.9	46.3
ICGV 93255	55.3	15.2	28.0	44.7
ICGV 93260	60.7	15.0	26.1	46.3
ICGV 93261	45.0	15.3	31.5	44.2
ICGV 93269	35.7	13.6	28.4	41.1
ICGV 93277	61.0	14.3	28.8	44.6
47-16	60.3	15.0	28.9	41.9
55-437	70.3	11.9	31.9	45.2
ICGS11	50.3	14.1	35.0	44.7
Kadiri-3	51.3	15.8	26.3	36.7
TMV2	70.7	13.3	34.8	44.3
TS32-1	62.3	16.6	34.4	42.2
Mean	56.0	14.1	30.1	43.0
SED($p<0.001$)	1.23	0.25	0.37	0.12

4.3.3 Pollen tube growth

The response of pollen tube growth to temperature was similar to that of pollen germination. Maximum pollen tube length was reached after 225 min. Observed and fitted values for pollen tube length are depicted in Fig. 4.3. The model parameters for the genotypes with their fits shown by R^2 are presented in Table 4.5. Pollen tube length in the twenty-one genotypes studied varied from 450 to 1450 μm (Table 4.6). Most genotypes recorded pollen tube length between 850-1050 μm. Genotype ICGV 93261 recorded the least pollen tube length of 450 μm, while 55-437 and ICGV 93232 recorded pollen tube lengths of 1410 and 1450 μm, respectively.

Genotypes showed significant differences in their T_{min}, T_{opt} and T_{max} temperatures obtained from modified bilinear equations (Table 4.6). Minimum temperature for pollen tube growth was similar to that for germination, and averaged to 14.6 ±3.5°C. Genotype ICGV 92120 and ICGV 93269 recorded lowest T_{min}, 11.9° and 12.4°C, respectively for pollen tube growth. Genotypes ICG 1236 (16.8°C) and TS 32-1 (18.0°C) had highest values of T_{min}. Average optimum temperature for pollen tube elongation, 34.6°C, was higher by 4°C than that required for pollen germination. The T_{opt} for genotypes ranged from 30.5° to 37.6°C. Genotypes ICGV 92116 and ICGV 93261 recorded lowest T_{opt} of 30.5°C, and genotypes 55-437 and ICGV 93255 recorded highest T_{opt}, 37.6° and 39.4°C, respectively.

Maximum or lethal temperature beyond which no pollen tube growth was observed averaged to 43.4°C, similar to that for pollen germination. Maximum temperatures (T_{max}) ranged from 37.5° to 46.5°C. Genotype ICGS 11 and ICGV 93277 had highest values of T_{max} 46.2° and 46.5°C, respectively.

No significant correlation could be observed for T_{min} versus T_{opt} or T_{max}. However a relatively high correlation of 0.40 was recorded between T_{opt} and T_{max}.

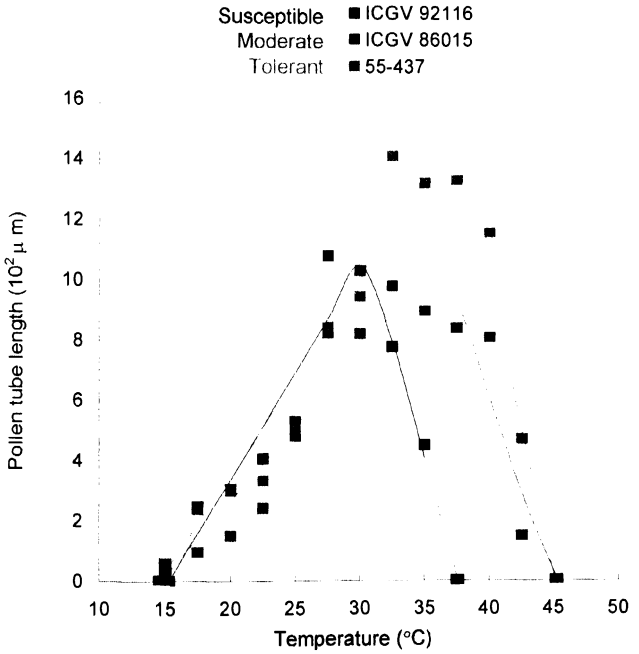


Fig. 4.3 Effect of temperature on pollen tube length of susceptible (T_{opt} < mean-LSD), moderately tolerant (T_{opt} = mean±LSD) and tolerant (T_{opt} > mean+LSD) genotypes. Symbols are observed values and lines fitted values.

Table 4.5 Model parameters from Newton-Gauss Maximum Likelihood Program in GENSTAT 5, describing pollen tube growth response to temperature between 10 ° and 47.5 °C.

Genotype	*a* ± s.e.	*b*1 ± s.e.	*b*2†	T_{opt}(±s.e.)	R^2 (n)
ICG 1236	12.61±0.972	-0.81±0.151	-0.88	36.4±1.06	87.6 (9)
ICGV 86015	10.76±0.780	-0.39±0.098	-0.39	35.0±1.01	86.2 (10)
ICGV 92109	12.84±0.543	-0.36±0.101	-0.36	34.0±0.53	95.2 (7)
ICGV 92113	12.42±0.704	-0.28±0.088	-0.84	34.4±0.86	89.2 (10)
ICGV 92116	10.92±0.735	-0.42±0.164	-1.13	30.5±0.80	89.1 (6)
ICGV 92118	11.88±0.626	-0.64±0.148	-1.20	33.5±0.63	93.5 (7)
ICGV 92120	10.28±0.291	-0.52±0.739	-0.95	35.1±0.39	97.3 (9)
ICGV 92121	12.05±0.339	-0.40±0.056	-0.40	34.1±0.38	97.4 (9)
ICGV 93232	13.95±1.200	-0.34±0.293	-1.05	35.8±1.21	84.6 (8)
ICGV 93233	11.48±0.792	-0.64±0.200	-1.13	36.8±0.72	86.3 (9)
ICGV 93255	8.38±0.312	-0.57±0.076	-1.93	39.1±0.32	92.7 (9)
ICGV 93260	11.95±0.889	-0.30±0.216	-0.86	34.9±0.82	72.3 (8)
ICGV 93261	5.89±0.918	+0.01±0.115	0.01	30.5±2.07	60.2 (7)
ICGV 93269	10.11±0.525	-0.22±0.064	-0.75	31.7±0.69	91.8 (8)
ICGV 93277	9.84±0.411	-0.18±0.068	-0.66	34.3±0.66	92.1 (9)
47-16	10.23±0.416	-0.31±0.067	-0.82	34.1±0.53	93.7 (8)
55-437	14.72±0.734	-0.61±0.193	-1.26	37.6±0.65	91.8 (10)
ICGS 11	9.40±0.804	-0.05±0.101	-0.69	33.5±1.18	82.1 (8)
Kadiri 3	9.63±0.797	-0.42±0.326	-0.42	34.1±0.55	85.1 (5)
TMV 2	10.48±0.588	-0.23±0.073	-0.71	34.0±0.81	92.2 (10)
TS 32-1	9.23±0.363	-0.15±0.056	-0.88	32.7±0.49	96.2 (7)

† b1 and b2 have same s.e. values

Table 4.6 Maximum pollen tube length and the three cardinal temperatures (°C) (from bi-linear fit) for *in vitro* pollen tube growth of groundnut.

Genotype	Maximum pollen tube length (μm)	Cardinal temperatures		
		T_{min}	T_{opt}	T_{max}
ICG 1236	1280	16.0	36.4	45.5
ICGV 86015	980	14.9	35.0	45.3
ICGV92109	1190	17.5	34.0	42.6
ICGV92113	1040	13.9	34.4	45.5
ICGV 92116	1080	15.3	30.5	37.7
ICGV 92118	1120	12.2	33.5	39.9
ICGV 92120	940	11.9	35.1	42.8
ICGV 92121	1090	13.4	34.1	42.8
ICGV 93232	1450	13.3	35.8	43.2
ICGV 93233	1110	13.6	36.8	43.3
ICGV 93255	860	15.2	39.1	44.7
ICGV 93260	1050	12.9	34.9	44.5
ICGV 93261	450	17.4	30.5	44.1
ICGV 93269	900	12.4	31.7	42.1
ICGV 93277	880	13.9	34.3	46.5
47-16	930	14.3	34.1	43.1
55-437	1410	14.5	37.6	45.1
ICGS11	920	18.9	33.5	46.2
Kadiri-3	850	15.0	34.1	37.5
TMV2	890	12.7	34.0	45.9
TS32-1	920	18.0	32.7	42.9
Mean	1020	14.6	34.4	43.4
SED($p<0.001$)	30.2	0.21	0.32	0.19

4.3.4 Pollen germination and pollen tube growth

There was a good relationship between values of T_{min} (R^2=0.35) and T_{max} (R^2=0.75) for pollen germination and for pollen tube growth. The relations indicate that genotypic values of T_{min} and T_{max} largely reflect the similar overall adaptation of plant processes for extreme temperatures, particularly lethal temperatures. The lack of correlation (R^2=0.003) between values of optimum temperatures (Fig. 4.4b) for pollen germination and tube growth indicates that there is independent genotypic variation in the response of germination and tube

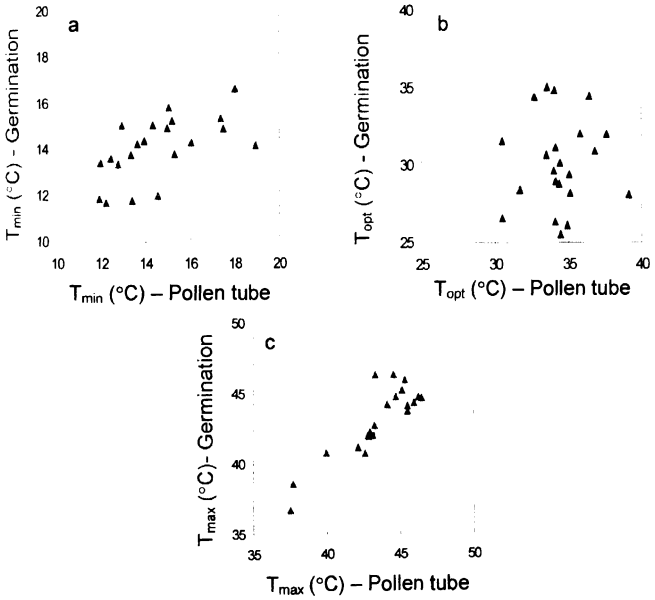


Fig. 4.4 Correlation between (a) T_{min}, (b) T_{opt} and (c) T_{max} temperatures for pollen germination and pollen tube growth for the 21 groundnut genotypes.

length to temperature and that at high value of T_{opt} for germination does not necessarily mean that tube length will also have high optimum temperature.

4.3.5 Rate of pollen tube growth

There was a strong linear relationship between the rate of pollen tube growth (expressed as reciprocal of time to 50% maximum length) and temperature in the sub-optimal temperature range (i.e. between T_{min} and T_{opt}), for pollen germination (Fig. 4.5). At higher temperatures, where the percent pollen germination was much lower, rates of pollen tube growth were very variable.

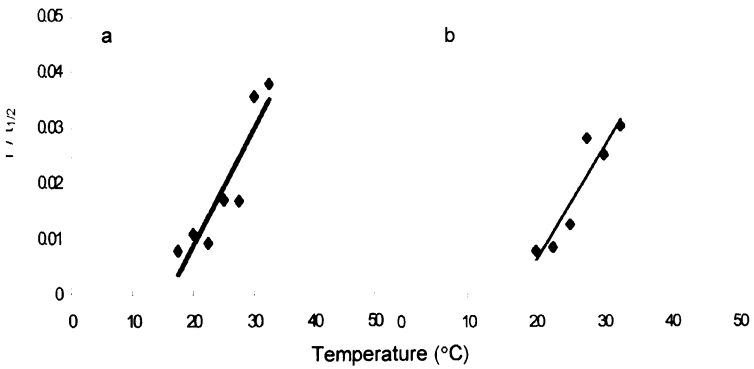


Fig. 4.5 Reciprocal of time to reach 50% of final pollen tube length versus temperature for genotypes (a) TMV 2 ($y = -0.033+0.0021x$; $R^2 = 0.84$) and (b) Kadiri 3 ($y = -0.0317+0.0019x$; $R^2 = 0.86$).

The rate of tube growth ranged from 4.5 to 31.4 μ min^{-1}, with an average of value of 12.7 μ min^{-1} (Table 4.7). Genotypes ICG 1236, 55-437 and TMV 2 all had significantly faster rates at optimum temperature by a factor >2 than most other

genotypes. Genotypes ICGV's 92116, 92118, 93260 and 93261 had pollen tube growth rates of <7 μ min^{-1}.

Table 4.7 Rate of pollen tube growth at the optimum temperature from linear fit for pollen tube growth for 21 groundnut genotypes.

Genotype	Rate of tube growth (μ min^{-1})
ICG 1236	26.3
ICGV 86015	18.6
ICGV 92109	9.0
ICGV 92113	7.8
ICGV 92116	6.7
ICGV 92118	6.9
ICGV 92120	9.1
ICGV 92121	11.9
ICGV 93232	7.0
ICGV 93233	10.8
ICGV 93255	17.9
ICGV 93260	6.3
ICGV 93261	4.5
ICGV 93269	7.0
ICGV 93277	8.0
47-16	10.1
55-437	28.9
ICGS11	11.0
Kadiri 3	15.9
TMV2	31.4
TS 32-1	12.4
Mean	12.7

4.3.6 Principal component analysis

A PCA analysis was carried out with the pollen germination and pollen tube length parameters, and RI, to characterise genotypic tolerance in response to high temperature. The parameters used included the values of T_{min}, T_{opt} and T_{max} for pollen germination (GERM) and pollen tube length (PTL), RI and $1/t_{1/2}$ PTL. To describe the response to high temperature, pollen germination (RGER) and tube length (RPTL) at 40°C were expressed relative to values at the optimum temperature.

The first three PCA scores accounted for 41, 24 and 12% of the variation, respectively (Table 4.8). The first PCA score discriminated genotypes with poor germination and rate of pollen tube growth, indicated by a large relative reduction in germination (RGER) and pollen tube length (RPTL) at 40°C. The first PCA score also accounted for genotypes with higher values of T_{max}GERM and T_{max}PTL. Therefore, genotypes with a positive score were susceptible to high temperature and those with a negative score tolerant.

The second PCA discriminated genotypes with high values for T_{min} for germination, high values for T_{min} for pollen tube length and high values for RI. Genotypes with positive score for second PCA were susceptible to high temperature and those with a negative score tolerant. The third PCA discriminated the genotypes with low values of T_{opt} for pollen tube length. The first and second PCA scores, along with the latent vectors, are plotted in Fig. 4.6. Latent vectors are the coefficients for principal components and are standardised

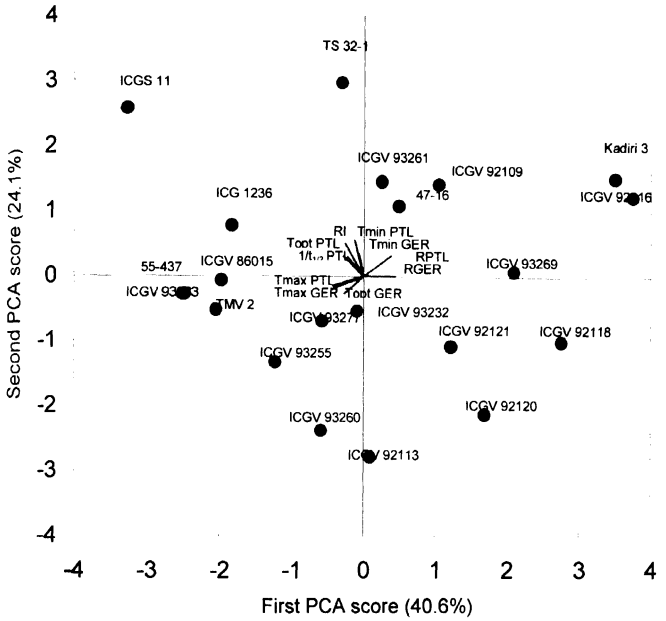


Fig. 4.6 First and second Principal Component Analysis (PCA) scores for the identification of genotype response to high temperature. The latent vectors are indicated by red lines showing the direction (angle) and magnitude (length). (RGER-reduction in pollen germination at 40 °C compared to values at optimum temperature; RPTL- reduction in pollen tube length at 40 °C compared to values at optimum temperature; T_{min}, T_{opt} and T_{max} are cardinal temperatures for pollen germination (GER) and pollen tube length (PTL); $1/t_{1/2}$PTL – reciprocal of time to establish 50% of pollen tube length).

so that the sum of the squares of the coefficients is unity for each one of them. Genotypes on the far left are classed as tolerant to high temperature and those on the far right are susceptible to high temperature. Genotypes ICG 1236, 55-437, TMV 2, ICGV 86015 and 93233 were all tolerant and exhibited similar temperature response characteristics. ICGS 11 also had similar characteristics to the previous group, but had low RI as well. The most susceptible genotypes were Kadiri 3 and ICGV 92116.

Table 4.8 Principal component analysis vectors of Axes 1, 2 and 3, and the variation accounted for by each axis. See text for description of parameters.

Parameter	Principal component vectors		
	Axis 1	Axis 2	Axis 3
RGER	0.44	-0.01	-0.05
RPTL	0.39	0.31	0.25
T_{min}GERM	-0.13	0.54	-0.21
T_{min}PTL	-0.27	-0.28	-0.02
T_{opt}GERM	-0.43	-0.15	-0.06
T_{opt}PTL	-0.07	0.34	-0.71
T_{max}GERM	-0.28	0.29	0.42
T_{max}PTL	-0.44	-0.21	-0.08
RI	-0.26	0.42	-0.03
$1/t_{1/2}$ PTL	-0.22	0.29	0.45
%variation	40.6	24.1	12.6

4.4 DISCUSSION

All biological processes respond to temperature and this response can often be described in terms of the rate (in the sub-optimal and supra-optimal range) and the cardinal temperatures: base or minimum (T_{min}), optimum (T_{opt}) and maximum (T_{max}) temperature. The current study shows very clearly that the processes of pollen germination and pollen tube growth can also be described in these terms.

The response to temperature of pollen germination and tube growth, and the estimated values for T_{min}, T_{opt} and T_{max} were similar to values reported for seed germination and other developmental and growth processes in groundnut (Mohamed, 1984; Ong, 1986). Values of T_{min}, T_{opt} and T_{max} for pollen germination ranged from 12-16°, 26-35° and 37-46°C compared with values of 8-12°, 29-37° and 41-47°C for seed germination (Mohamed, 1984). Pollen tube length had slightly higher values of T_{min} (12-18°C), but similar values for T_{opt} and T_{max}. This 'universal' response to temperature, particularly at the upper and lower extremes of the range is to be expected given the biochemical basis of rate response to temperature (Johnson and Thornley, 1985).

Pollen germination and pollen tube growth occur very rapidly in groundnut. The maximum percentage pollen germination occurred within 25 to 30 min and pollen tubes attained 75 to 80% of their maximum length within 45 min. The rate of pollen tube elongation ranged from 5 to 30 μ min^{-1} and the maximum pollen tube lengths (at T_{opt}) from 450 to 1450 μ. Rapid germination and tube growth is an adaptive response to the unique flowering habit of groundnuts. In groundnut, the

flower buds develop very rapidly during the night and open soon after dawn; and by midday, flowers wither (Pattee and Mohapatra, 1986). The open flower is borne on a unique structure called hypanthium, which may vary in length from 2.5 to 7.5 cm (Lu, 1990). The ovary is situated at the base of hypanthium. Rapid germination and pollen tube growth is therefore essential if pollen tubes are to reach the ovary and fertilisation to occur before flowers wither and when environmental conditions are most favourable to the plant at the start of the day.

Values of T_{opt} for germination and tube growth were between 26°-35°C and 30°-36°C, respectively and temperatures warmer than these significantly reduced the number of pollen grains germinating and the length of the resultant pollen tubes. Pollen germination was particularly sensitive to warm temperatures of 35°C or more, with lethal temperatures as low as 37°C in Kadiri 3. Fruit-set in groundnut, is also susceptible to high temperature and the floral temperature above which temperature reduces fruit-set is about 34°C in ICGV 86015 (Vara Prasad *et al.*, 1999a, 2000a). This is wholly consistent with the observed effects of temperature on pollen germination and tube length for ICGV 86015, where Topt for germination and tube growth were 29.4° and 35.0°C, respectively.

Groundnut genotypes also differed in leaf membrane thermostability or RI (described as 100-RI, such that higher values of RI describe greater tolerance). Membrane thermostability has been used by Ketring (1985) and Chauhan and Senboku (1997) to identify temperature tolerance in groundnut. Based on RI

values, the most heat tolerant genotypes in the current study were ICG 1236 and 55-437, that had RI values >45% and double that of the overall mean RI of 22%.

Similar values (47 and 50%) have been recorded for ICG 1236 by Srinivasan *et al.* (1996) and Talwar *et al.* (1999). These two cvs are therefore considered heat tolerant. Cultivar 55-437 is a drought-tolerant cv. widely grown in the sub-Saharan Africa while other cvs. with high RI values such as TMV 2 (30%) and ICGS 11 (35%) are widely grown in drought prone regions of India. Heat tolerance *per se* may therefore be an important component of overall tolerance to environments prone to abiotic stress, as Greenberg *et al.* (1992) suggested.

Pollen germination is the process most closely associated with the stability of the pollen cell membrane, and there was a positive relationship between RI and pollen germination (Fig. 4.7). Pollen germinates only when the cell membrane is intact and disruption of the membrane due to stress results in the failure of germination (Shivanna and Sawhney, 1997). This injury to cell membrane would also reduce photosynthesis, respiration and other membrane associated mechanisms.

Evidence from other crops suggests that tolerant genotypes selected by this test perform well and give stable yields in hot environments. For instance, Saadalla *et al.* (1990) reported that heat tolerant genotypes of wheat, determined based on electrolyte leakage, outyielded sensitive ones by 19% under field conditions. Kuo

et al. (1981) showed that vegetable species with low RI were more stable in different growing seasons.

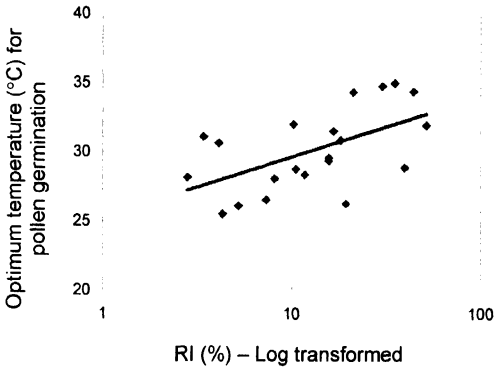


Fig. 4.7 Relation between percentage relative injury values for membrane thermostability and optimum temperature for pollen germination (y = 1.9231Ln(x) + 25.215; R^2=0.32).

The difference in genotype tolerance can be accounted for the greater tolerance or adaptability of pollen to high temperature, due to presence of heat shock proteins or due to rapid synthesis of heat shock proteins on exposure to high temperature. In a study with groundnut cultivars (ICG 1236, ICGS 44 and Chico) Talwar and Yanagahira (1999) attributed the greater tolerance of ICG 1236 to the presence of proline, a cellular amino acid. Proline has been shown to induce tolerance in pollen of several crop plants including, cowpea (Mutters *et al.*, 1989), and *Petunia* and *Lilium longiflorum* (Qi and Croes, 1983). In these crops, greater the amount of proline in pollen, greater is the tolerance to high temperature as up to 50% of the cytoplasmic proline is used for protein synthesis during pollen tube elongation (Qi and Croes, 1983). Along with proline, crop

plants (e.g. sorghum, barley) are also known to synthesize HSPs on exposure to heat stress that are in the range of 16 – 25 kDa and 70 – 84 kDa (Howarth, 1991). Hence, studies in groundnut are necessary to identify presence of these proteins and the associated genes for developing heat tolerant varieties.

There was considerable genotypic variation in the cardinal temperatures for pollen germination and tube length, rate of pollen tube length and RI, which may contribute to variation in heat tolerance. The Principal Component Analysis (PCA) was used to characterise and group genotypes for their pollen responses to temperature and RI values. The first PCA identified tolerant and susceptible genotypes based largely on their relative ability of pollen to germinate and grow at supra-optimal temperatures. Genotypes 55-437, TMV 2, ICG 1236, ICGV 86015 and ICGV 93233 were all classed as heat tolerant on this basis, and this classification accords with the wider adaptation of these genotypes (55-437 in Sudano-Sahelian region and TMV 2 in SAT of India). In contrast, Kadiri 3, ICGV's 92116, 92118 and 93269 were all susceptible to heat. In 92-series of ICRISAT, ICGV lines are all tolerant drought-breeding lines that mostly have little tolerance to temperature.

Pollen germination and pollen tube growth of the genotypes under high temperatures can be used as a screening tool in selecting heat tolerant genotypes. This simple technique requires less input than screening entire plants. Its advantage is that it can be used as a tool to select heat tolerant genotypes in the field at the most sensitive stage, i.e. flowering. Such screening

techniques also help the breeder to select the heat tolerant parents for quickly advancing them into next generation.

4.5 CONCLUSIONS

Groundnut genotypes differ in their tolerance to temperature based on membrane thermostability, pollen germination and pollen tube growth. General tolerance to high temperature, identified by membrane thermostability in this study, was found to extend to specific reproductive processes like pollen germination in groundnut. Of the genotypes tested, ICG 1236, 55-437 and TMV 2 are consistently tolerant to high temperature for the processes studied and can be used for cultivation in areas with high temperatures during crop season or for breeding heat tolerant groundnut genotypes.

CHAPTER 5

ACCLIMATION TO HIGH TEMPERATURE IN GROUNDNUT

5.1 INTRODUCTION

Heat stress studies conducted so far with groundnuts have shown that a sudden imposition of high temperature, during the sensitive reproductive phase, reduces fruit set and yield (Ketring, 1984; Wheeler *et al.*, 1997, Vara Prasad *et al.*, 1998; 1999a). However, under natural conditions in the field temperature changes are more gradual (e.g. over a number of days). It is possible that acclimation to high temperature may occur during the day and over the period of temperature increase. Hence, heat acclimation may enable plants to reduce the effects of heat injury.

Heat acclimation, also known as acquired thermotolerance or heat hardening (Henle and Dethlefsen, 1978), is the ability of organisms to tolerate normally lethal high temperatures due to an initial exposure to high but not lethal temperature. Alternatively, it has been defined as the ability of plants to increase their tolerance to heat following exposure to acclimation temperatures (Li *et al.*, 1991). Levitt (1980) suggested that thermal tolerance of different genotypes should be compared when plants are at the acclimated stage because the ability of genotypes to tolerate high temperature is significantly and differentially affected by their heat acclimation potential.

Response to acclimation temperature prior to heat stress varies with the crop and genotype. It has been shown following the imposition of acclimation temperatures early in the growth cycle in wheat that yield was reduced less in a heat sensitive variety without any improvement in the heat tolerant cultivar (Stone and Nicolas,

1995). In common bean (Li *et al.*, 1991) acclimation temperature increases the tolerance, and causes less reduction in yield, of genotypes subsequently exposed to high temperature episodes at later stages of the growth cycle. It is therefore important to determine whether acclimation at different stages of development affects fruit set in groundnuts, and particularly whether processes affecting fruit-set (e.g. pollen production, germination, pollen tube growth) can acclimate.

Heat injury during flower development in cowpea was associated with decreased proline accumulation in pollen and greater accumulation of proline in the anther wall (Mutters *et al.*, 1989). Studies indicate that a gradual increase in temperature permits not only a far greater protein synthesis at 50 °C but also that the proteins synthesised at this temperature include heat shock proteins - HSPs (Howarth, 1991). Pollock and Howarth (1990) also suggest from their studies that sub-lethal heat shock pre-treatment induced thermotolerance in sorghum. Such studies have not been conducted in groundnuts, and if such thermotolerance exists in groundnuts, it could be exploited in breeding genotypes for stress environments.

The objectives of this study were: (1) to determine the effect of acclimation prior to high temperature episodes at pre-anthesis and post-anthesis stages of development on fruit-set in contrasting groundnut genotypes; and (2) to investigate whether the acclimation during vegetative or floral bud development affects pollen germination at high temperature.

5.2 MATERIALS AND METHODS

5.2.1 Cultivars

Two groundnut cultivars were used in this study, 55-437 (heat tolerant) and ICGV 92116 (heat sensitive). The relative tolerance of these genotypes to high temperature based on membrane thermostability and pollen response to temperature was established in Chapter 4. Their responses to a short period of high temperature at flowering were also established in a screening experiment conducted at Plant Environment Laboratory, The University of Reading, Reading, UK in 1999 (Craufurd *et al.*, unpublished).

5.2.2 Plant Culture

Seeds of groundnut were germinated in module trays with compost as growth medium at 28°/22°C (day/night). Seedlings of similar physiological age were then transplanted to pots of 2 L volume (10 cm diameter x 15cm height). Pots were filled with a standard soilless mixture containing sand, gravel, vermiculite and loamless peat compost in proportions of 4:2:2:1 by volume, respectively. A commercial controlled release fertiliser (0.15 kg kg^{-1} N, 0.10 kg kg^{-1} P, 0.12 kg kg^{-1} K, 0.02 kg kg^{-1} MgO plus trace elements, Osmocote Plus, (Scotts UK Ltd, UK) was incorporated into the mixture at the manufacture's recommended rate of 5 g L^{-1}.

Plants were grown in artificially lit (700 μmoles m^{-2} s^{-1}) growth chambers at 28°/22°C, with a 12h photo-and thermo-period. There were five replicate plants and these were moved around daily in the chamber to reduce locational effects.

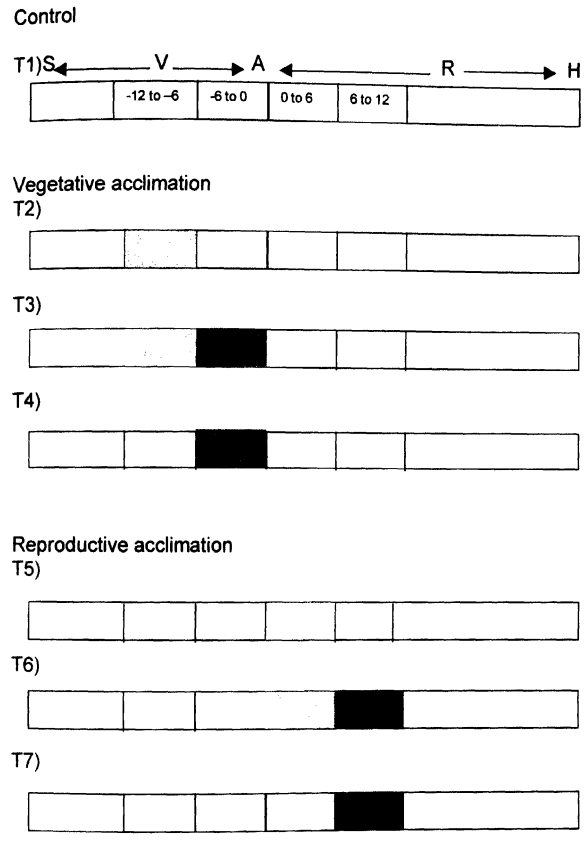
Plants were watered manually everyday to maintain the water content at field capacity.

5.2.3 Temperature treatments

Studies have shown that temperatures of around 35°C can be used as an acclimation temperature for groundnut genotypes (Srinivasan *et al.*, 1996; Talwar *et al.*, 1999). Any temperature above 35°C is known to cause reductions in pod number (Vara Prasad *et al.*, 1999a) and hence a temperature of 40°C was selected to study the groundnut genotypic responses to high temperature. All temperature treatments imposed are depicted in Fig.1. In all the treatments, VPD was maintained close to 2 kPa throughout the experimental period. Plants exposed to high temperature were watered twice daily to ensure adequate soil moisture.

5.2.3.1 Vegetative acclimation

Plants were grown continuously at 28°/22°C, except during the temperature treatment periods. Plants were exposed to an acclimating temperature of 34°/22°C during the 6 d period (12 to 6 DBA) prior to initiation of microsporogenesis. Plants were then exposed to high temperature of 40°/22°C for a period of 6 d (6 to 0 DBA). During this treatment, only vegetative growth was exposed to acclimation temperature and flower buds along with vegetative growth were exposed to high temperature.



(S = Sowing; V = Vegetative; A = Anthesis; R = Reproductive; H = Harvest)
(☐ =Control at 28/22 °C (day/night); = Acclimation at 34/22 °C; ▮ = High temperature stress at 40/22 °C)

T1 – Overall control (Con)
T2 – Acclimation of vegetative period (12 to 6 DBA) – Vegetative acclimation (VA)
T3 – T2 + HT stress 6 to 0 DBA (VA+VHT)
T4 – Control of HT stress in T3 (VHT)
T5 – Acclimation of reproductive period (0 to 6 DAA) – Reproductive acclimation (RA)
T6 – T5 + HT stress 7 to 12 DAA (RA+RHT)
T7 – Control of HT stress in T6 (RHT)

Fig. 5.1 Temperature treatments imposed at different stages of groundnut development.

5.2.3.2 Reproductive acclimation

Plants were grown continuously at 28°/22°C, except during the temperature treatment periods. Reproductive acclimation was achieved by exposing plants to 34°/22°C from 0 to 6 DAA. Plants were then exposed to high temperature of 40°/22°C for a period of 6 d. Both flower buds and flowers were therefore exposed to high temperature in this treatment. Flowers produced before or after high temperature treatment were manually removed early in the morning.

Plants exposed to only high temperature treatment were moved directly from control to high temperature chambers on the night prior to their exposure to high temperature. Similarly, all transfers were done after the day treatment was completed.

5.2.4 Measurements

Leaf and flower bud temperatures were measured on three plants of each genotype under control, acclimated and high temperature environments. Leaf temperatures were recorded by attaching a copper-constantan thermocouple to the abaxial surface of the leaf. Flower bud temperature was measured by inserting a micro copper-constantan thermocouple into the bud. Temperatures were logged at 10 s intervals and averaged for every 15 min using a Delta T logger. Temperature and radiation levels in the growth chamber were also logged with a similar device.

The temperature of the buds in both the genotypes were consistently and systematically lower than the air temperatures (Fig.5.2). Bud temperatures were lower than air temperature by 1°C under optimum (28°/22°C) conditions, 1.3°C under acclimation (34°/22°C) and 2.5°C under high temperature (40°/22°C) conditions.

5.2.4.1 Vegetative acclimation

In the pre-microsporogenesis treatment, daily flower production was recorded from first flower appearance to until 6 DAA. Flowers were tagged daily, during the six day period of counting, with the date of flower emergence recorded on tags in all the treatments. Flowers arising at a node that was already tagged were removed to ensure that only one tagged flower remained at a node.

5.2.4.2 Reproductive acclimation

In the pre-anthesis treatment, flowers were counted during the 6 d period of the high temperature treatment. Flowers were tagged daily, during the six day period of counting, with the date of flower emergence recorded on tags in all the treatments. Flowers arising at an already tagged node were removed which ensured that only one flower was allowed at a node. All flowers borne after the 6 d period of tagging were also removed.

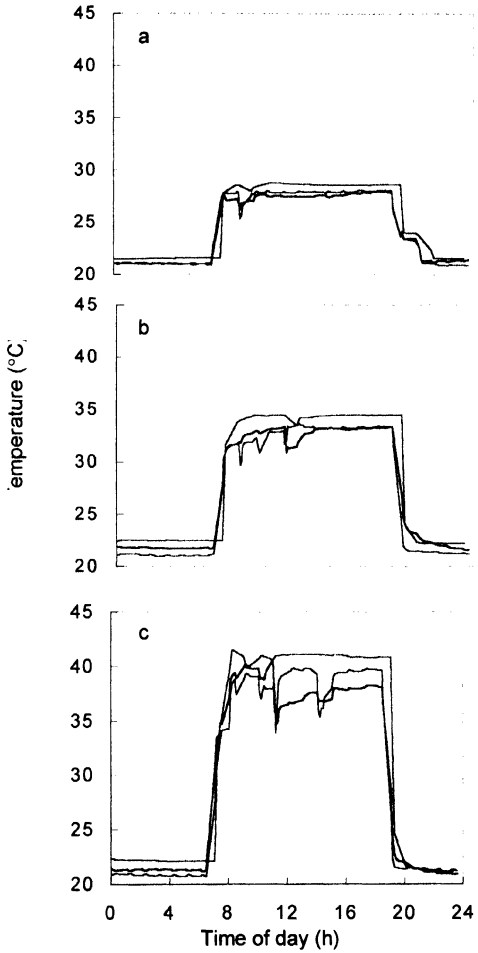


Fig. 5.2 Diurnal cycle of air (red line) and floral bud temperature of ICGV 92116 (blue line) and of 55-437 (pink line) over a 6 d period in growth cabinets under (a) 28/22 °C (optimum temperature); (b) 34/22 °C (acclimation temperature) and (c) 40/22 °C (high temperature).

5.2.5 Pollen viability

During the 6 d period, when flowers were tagged both in vegetative and reproductive treatments, pollen was collected every day from flowers and assessed *in vitro* for pollen germination as described in Chapter 4, section 4.2.6.

5.2.6 Harvest

Plants were harvested 10 d after the high temperature treatment was withdrawn. This allowed time for peg formation in all the tagged flowers. Pegs formed from flowers at nodes that were tagged were recorded. Each plant was separated into leaf and stem, pegs, and roots. These were dried in oven at 80°C for 3-4 d and dry weights were recorded.

5.2.7 Statistical analysis

Shoot dry weight, root dry weight, flower number produced during the 6 d of tagging, pegs produced from these tagged flowers, and percent fruit-set were analysed by Two-way ANOVA in GENSTAT 5 (Genstat 5 Committee, 1997) using five replications (or five plants). Fruit-set was calculated as ratio of the number of pegs produced after 10 days of tagging to total number of tagged flowers during 6 d period. Shoot and root dry weight were log transformed before analysis. Similarly, percent fruit-set was subjected to angular transformation to ensure homogeneity of variances.

5.3 RESULTS

5.3.1 Response to vegetative acclimation

5.3.1.1 Shoot dry weight

No significant interaction was observed between the temperature treatments and genotypes; only the main effects of temperature treatments and genotypes were significant. Shoot dry weight was reduced significantly when exposed to either VA, VHT or to VA+VHT treatments (Fig. 5.3), but with no significant difference among these three temperature treatments.

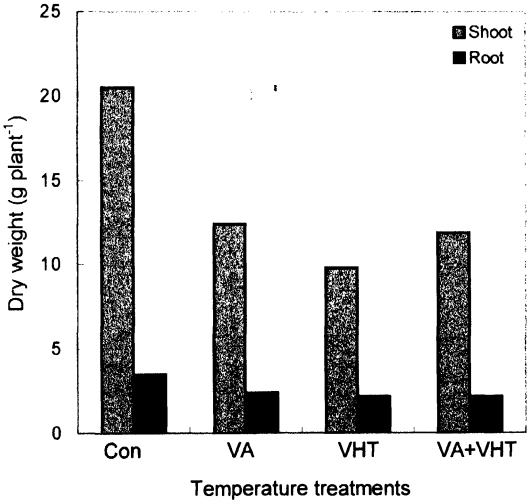


Fig. 5.3 Effect of vegetative acclimation (VA-34/22 °C – 6 to 12 DBA), vegetative high temperature (VHT-40/22 °C – 0 to 6 DBA) and VA+VHT compared to control (28/22°C) on shoot and root dry weight. Data are mean of two genotypes.

Acclimation treatment (VA), VHT, VA+VHT treatments reduced shoot weight by 37, 50 and 43%, respectively, compared to the control. Genotype ICGV 92116 had 42% more shoot dry weight than 55-437 (Fig. 5.4).

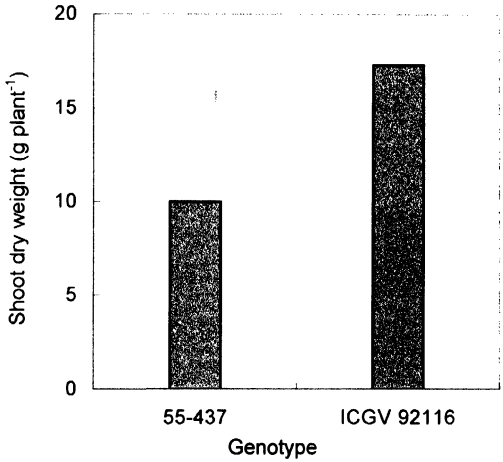


Fig. 5.4 Genotypic differences in shoot dry weight, averaged over all the treatments, recorded at 10 d after end of tagging. Data are mean of temperature treatments.

5.3.1.2 Root dry weight

There was no difference between genotypes and the temperature x genotype interaction was not significant for root dry weight. However, temperature significantly ($p<0.001$) reduced root weight (Fig. 5.3). The effect of VHT or VA + HT did not differ significantly from VA, which reduced root weight by 32%. Root dry weight was around 20% of the total dry weight.

5.3.1.3 Flower number

There were no significant effects of temperature or temperature x genotype interaction on flower production following the 6d period of high temperature (VHT). However, genotypes differed significantly for flower number, with 55-437 producing 24% more flowers than ICGV 92116 (Fig. 5.5).

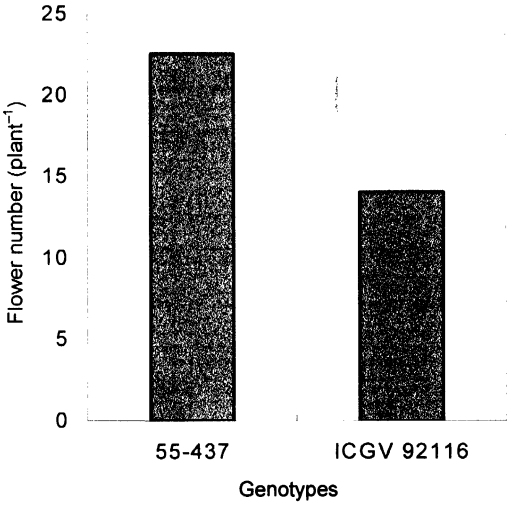


Fig. 5.5 Genotypic differences for total flower number produced during the first 6 d after anthesis. Data are means of temperature treatments.

5.3.1.4 Fruit-set

There was a significant ($p<0.001$) interaction between temperature and genotypes on fruit set (Fig. 5.6). Both genotypes recorded about 70% fruit set at the control (28°/22°C) temperature. Acclimation temperature during vegetative

period (VA) significantly increased fruit-set in both genotypes, though the increase was greater (22%) in 55-437 than in ICGV 92116 (12%).

The imposition of VHT treatment from 0 to 6 DBA significantly ($p<0.001$) reduced fruit-set in ICGV 92116 (by 22%), but not in 55-437. However, when VHT was preceded by VA, fruit-set in 55-437 was increased significantly ($p<0.001$) by 16% compared to control treatment. In contrast, in ICGV 92116 fruit-set was significantly reduced by 10% compared to control treatment. Thus, 55-437 recorded 26% more fruit-set than ICGV 92116 when VA was followed by VHT.

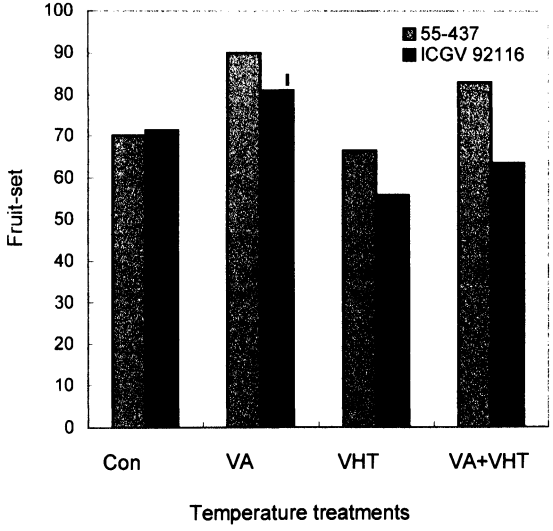


Fig. 5.6 Effect of vegetative acclimation (VA: 34/22°C; 6 to 12 DBA), high temperature (VHT: 40/22°C; 0 to 6 DBA) and VA+VHT compared to control on fruit-set (% angular transformed). Data are mean of genotypes studied.

5.3.2 Response to reproductive acclimation

5.3.2.1 Shoot dry weight

Temperature treatments, whether RA, RHT or RA+RHT did not significantly affect shoot dry weight. Neither the main effect of temperature nor the interaction between temperature and genotype were significant. However, genotypes differed significantly in their dry weights. ICGV 92116 accumulated 25% more shoot dry weight when compared to 55-437 under similar conditions (Fig. 5.7).

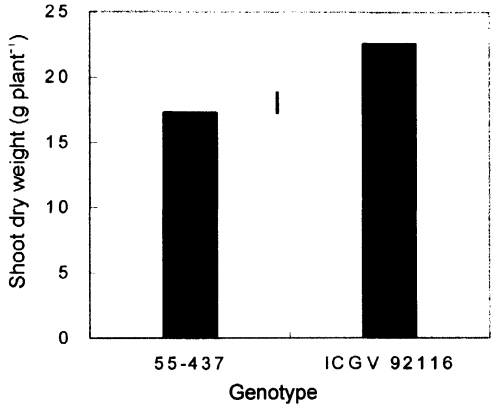


Fig. 5.7 Genotypic differences in shoot dry weight recorded at 10 d after end of tagging. Data are mean of temperature treatments.

5.3.2.2 Root dry weight

There was a significant ($p<0.001$) temperature x genotype interaction for root dry weight. Root dry weight was reduced by RA and RHT treatments in both genotypes, but the effect was much greater in ICGV 92116 than in 55-437. Genotype ICGV 92116 had twice as much root dry weight as 55-437 in control, but RA, RHT and RA+RHT treatments reduced dry weight by 57, 32 and 63%,

respectively. In contrast, in 55-437 root dry weight was not significantly reduced by the RA or RHT treatments.

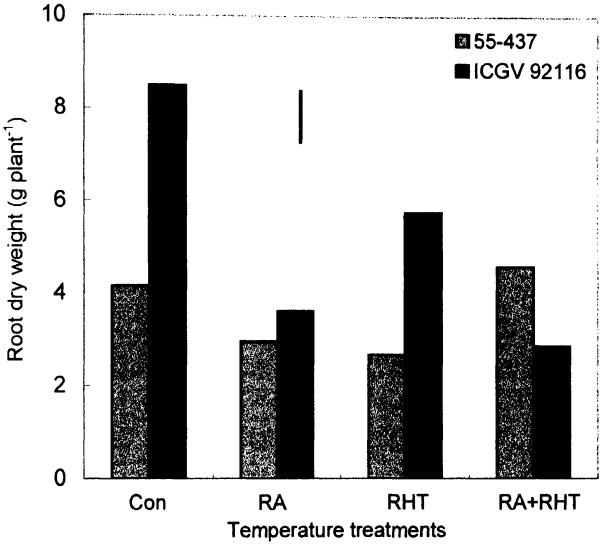


Fig. 5.8 Root dry weight of groundnut genotypes, 55-437 and ICGV 92116, exposed to different temperature treatments during the post-anthesis period (0 to 12 DAA).

5.3.2.3 Flower number

Genotypes ICGV 92116 and 55-437 produced about 25 flowers per plant during the 6d period following anthesis. Temperature had a significant effect on flower production in ICGV 92116 and flower number was reduced to 12, 16 and 8 in RA, RHT and RA+RHT treatments, respectively. In contrast, in 55-437, flower production was not significantly affected by temperature.

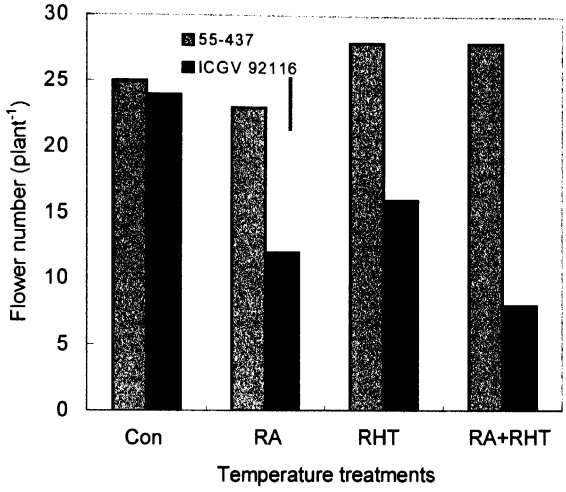


Fig. 5.9 Flower number produced in groundnut genotypes, 55-437 and ICGV 92116 during the 6 d period of tagging following exposure to different temperature treatments during the pre-anthesis period (0 to 12 DAA).

5.3.2.4 Fruit-set

There was a significant interaction ($p<0.001$) between temperature and genotype for fruit-set during the post-anthesis period. Acclimation treatment (RA), but not RHT or RA+RHT, caused a slight, but significant reduction in fruit set in 55-437 (Fig. 5.10). In ICGV 92116, both RA and RHT treatments caused a significant reduction in fruit-set of about 16%. However, RA+RHT treatment resulted in a significant increase, not a decrease, in fruit-set.

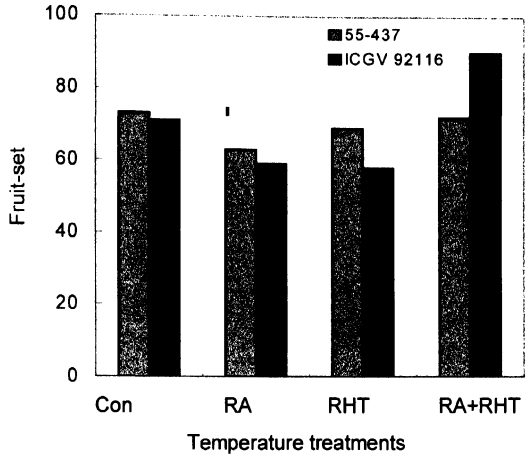


Fig. 5.10 Effect of reproductive acclimation (RA: 34/22°C; 0 to 6 DAA), high temperature (RHT: 40/22°C; 6 to 12 DAA) and RA+RHT compared to control on fruit-set (% angular transformed). Data are mean of genotypes studied.

5.3.3 Pollen viability

Pollen viability is reported here in terms of percentage pollen germinated on exposure to a given temperature treatment. Pollen collected from plants exposed to different temperature treatments during vegetative (VA, VHT and VA+VHT) and reproductive (RA, RHT and RA+RHT) periods were used for testing pollen viability. The pollen collected from plants exposed to these various treatments and control was exposed to a series of temperature treatments from 10° - 45 °C, at 5°C interval and pollen germination was recorded (Fig. 5.11).

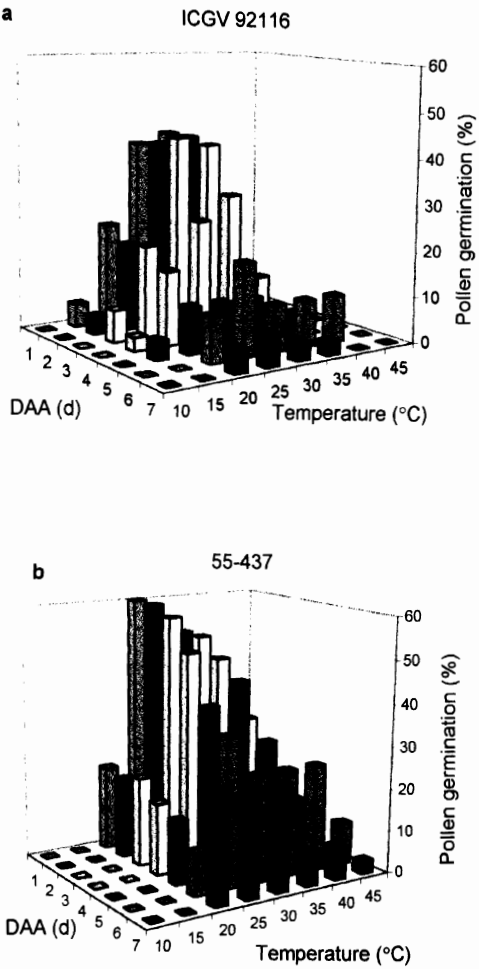


Fig. 5.11 Daily percentage pollen germination on *in-vitro* germinating medium of temperatures ranging from 10 to 45°C at 5°C interval in genotypes ICGV 92116 (a) and 55-437 (b) for a period of 7 d starting from 7 DAA exposed to control temperature (28/22°C).

The pattern of pollen germination over the 6 d period at temperatures of 10° to 45°C was similar in both genotypes (Fig. 5.11). However, the pollen germination in the heat susceptible ICGV 92116 was lower than in heat tolerant 55-437 throughout the study, even under control conditions (Fig. 5.12). In both genotypes optimum temperature for pollen germination was between 25° and 30°C. Less than 10% of pollen germinated at 10 or 15°C. At high temperature, >35°C, significantly more pollen germinated in 55-437 than in ICGV 92116 (Fig. 5.12d and h; Table 5.1). In both genotypes, the percentage of pollen germinated declined over the 6 d period of observation. Pollen collected from ICGV 92116 plants exposed to high temperature, during post-anthesis stage, irrespective of the previous treatment, had a high proportion of the pollen grains that were deformed, shrunk or denatured (Plate 5.1). This would have resulted in low pollen germination in this genotype.

The acclimation treatments VA and RA (Fig. 5.11b and f), and high temperature VHT and RHT (Fig.5.11c and g) treatments, significantly reduced pollen germination in ICGV 92116. In contrast, 55-437 was clearly much more tolerant for acclimating and high temperatures (Table 5.1). High temperature during pre-anthesis stage reduced pollen germination in both the genotypes, but more in ICGV 92116. On the other hand, high temperature during post-anthesis stage had a moderate effect on 55-437 but severely reduced the pollen germination in ICGV 92116.

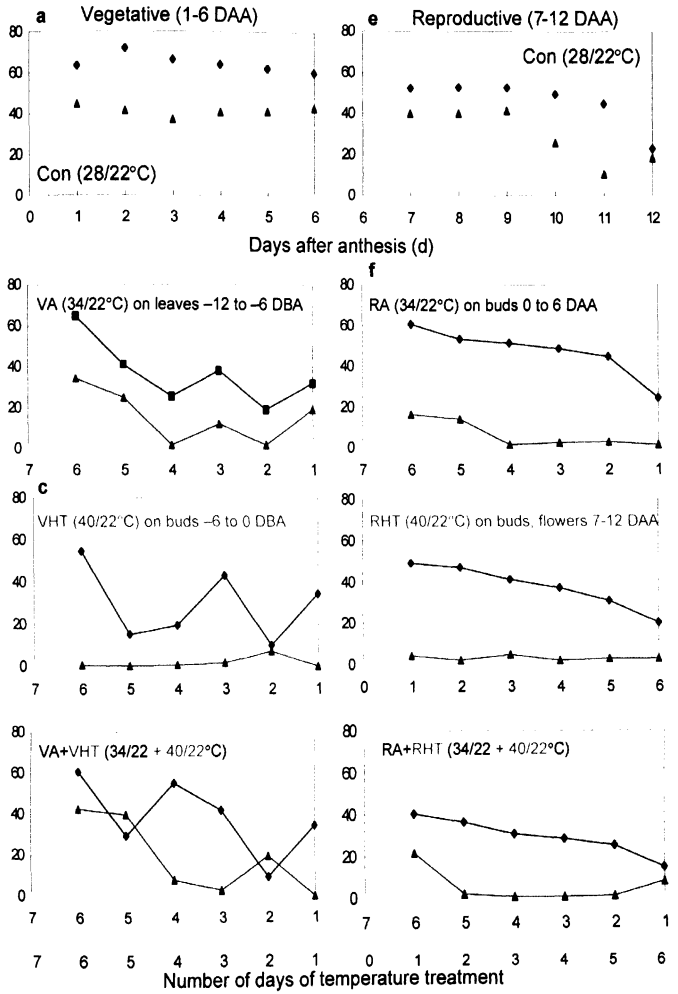


Fig. 5.12 Daily *in vitro* percentage pollen germination at 30°C in genotypes ICGV 92116 – heat susceptible (▲) and 55-437 – heat tolerant (♦) during the period 0 - 6 DAA (a, b, c and d) and in the period 7-12 DAA (e, f, g and h) exposed to different temperature treatments. (X-axis key: Black – number of days after anthesis; Blue – number of days of 34/22°C; Red – number of days of 40/22°C).

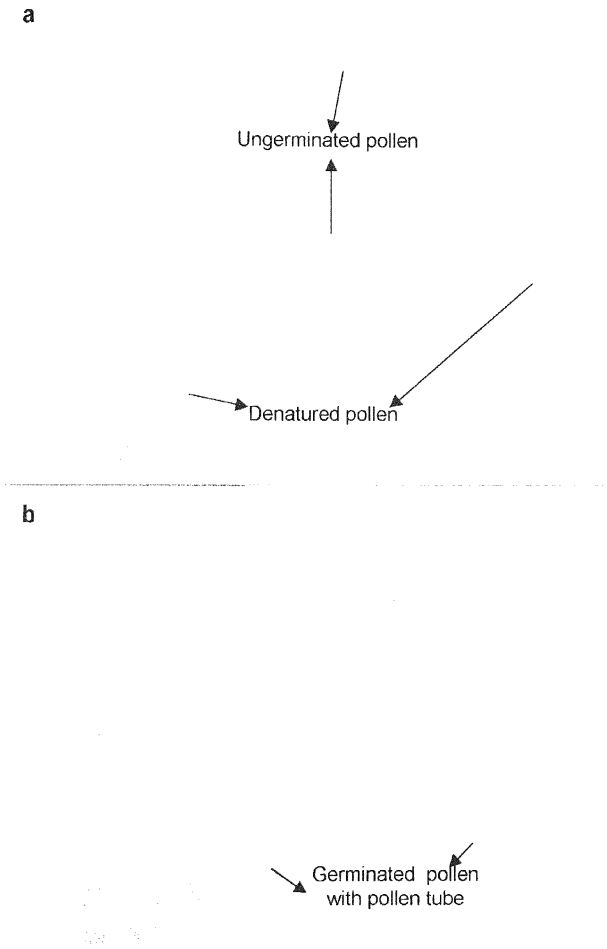


Plate 5.1 Pollen collected from flowers of groundnut genotypes (a) ICGV 92116 and (b) 55-437, exposed to a temperature of 40/22°C during the reproductive period.

Table 5.1 Percentage pollen germination in genotypes ICGV 92116 and 55-437 during the 6 d period during 0-6 DAA and 7-12 DAA exposed to different temperature treatments.

Temperature treatment	Pollen germination (%)	
	ICGV 92116	55-437
----------0-6 DAA----------		
Con 0-6 (28/22°C)	41.2	64.6
VA (34/22°C)	15.6	34.8
VHT (40/22°C)	18.9	38.6
VA+VHT	1.7	29.5
SED	0.42	
----------7-12 DAA----------		
Con 7-12 (28/22°C)	29.3	45.7
RA (34/22°C)	6.3	47.2
RHT (40/22°C)	5.7	29.3
RA+RHT	2.9	37.4
	0.47	

Vegetative exposure of ICGV 92116 plants to acclimating temperature (Fig. 5.12 b and d) appears to have induced some tolerance in pollen germination when compared to similar treatments during the reproductive stage. This acclimation was visible for the pollen that was exposed for 5 or 6 d to pre-anthesis acclimation temperature.

5.4 DISCUSSION

In this study, acclimation (34°C) and high (40°C) temperatures were imposed at pre- and post-anthesis, and had contrasting effects on root and shoot growth, flower production, fruit-set and pollen germination. There were also significant differences between genotypes, particularly for the post-anthesis treatments, and so the discussion will initially focus on ICGV 92116.

Vegetative acclimation (VA) and high temperature (VHT) reduced growth of root and shoot, of both genotypes. In contrast, RA and RHT treatments had no effect on shoot growth, but did significantly reduce root growth. This reduction in root, but not shoot growth may be explained based on the 'functional equilibrium' theory of Brouwer (1983). The theory states that plants shift their allocations towards shoot if carbon gain of the shoot is impaired by a low level of above ground resource, such as light or CO_2. In this study above ground temperature is a limiting factor. More shoot assimilates are required to account for increased respiration and transpiration (to maintain leaf temperature) of the shoot (Bjorkman *et al.*, 1980) and hence assimilate supply to the root is limited. Shoot weights were 30-50% higher in the post-anthesis than pre-anthesis treatment, which is indicative of a larger shoot leaf area and heat load.

In addition to 'functional equilibrium', groundnut membrane thermostability is more sensitive during the vegetative than during the reproductive stages to high temperature (Srinivasan *et al.*, 1996). This disrupts the membrane system, e.g. thylakoid membranes, of the photosynthetic apparatus (Raison *et al.*, 1980), thus

limiting the available assimilates for plant growth. Hence, a greater reduction in assimilate production occurs during the vegetative phase than during the reproductive phase, which explains the decrease of both root and shoot in vegetative phase and of only root growth during the reproductive phase.

Other reasons for the reduction in root weight may be related to ontogenetic effects on root growth or sensitivity to high temperature. Root growth in groundnut declines during the reproductive period, and this decline occurs sooner at higher temperature because of the greater thermal time accumulated (Wheeler *et al.*, 1997). Therefore high temperature during the reproductive period, when roots are growing less actively than during vegetative period, may hasten this ontogenetic decline.

Acclimating and high temperatures had no effect on flower production, and positive effects (VA) or negative effects (VHT) on fruit-set in both the genotypes. However, RA, and particularly RHT treatments, significantly reduced flower production and fruit-set in ICGV 92116. These responses can be explained by the known responses of groundnut flower production, fruit-set to temperature, and corroborated by observed effects on pollen germination.

Flower production in groundnuts is sensitive to high temperature during the post-anthesis phase and flower number is reduced by approximately 2 flowers per plant $°Cd^{-1}$ above 30°C (Vara Prasad *et al.*, 1998). The reduction in flower number at 40°C to about 15 flowers per plant is similar to that observed for ICGV

86015 (Vara Prasad *et al.*, 1998) at this temperature. High temperature during the pre-anthesis phase does not directly increase flower production in the post-anthesis phase, unless vegetative growth and hence node production is accelerated.

Fruit set is also highly sensitive to temperature above the threshold value of 34°C and no fruit is set at about 42°C in ICGV 86015 (Vara Prasad *et al.*, 2000a). In this study, acclimation temperature was 34°C and high temperature 40°C. So acclimation should have had little or no affect on fruit-set. High temperature treatment, on the other hand, should have significantly reduced fruit-set. These responses are due both to effects during floral bud development (i.e. at microsporogenesis) and during pollination (Vara Prasad *et al.*, 1999b). Acclimating temperatures during the pre-anthesis phase occurred before microsporogenesis, and hence had no effect on fruit set. However, high temperature during the pre-anthesis phase (0-6 DBA) and acclimating and high temperatures during the post-anthesis phase, all reduced fruit set in ICGV 92116. This suggests that the critical temperature for ICGV 92116 is <34°C, while the critical temperature for 55-437 is close to 40°C.

The observed effects of high temperature on pollen germination explain the observed effects on fruit set in the genotypes. The decline in pollen germination with increase in plant age was attributed to decreased pollen number and differences in genotype percentage pollen germination was attributed to the relative concentrations of the amino acid proline in anthers by Talwar and

Yanagahira (1999) in groundnut genotypes. Studies in major crop plants have established the role of proline in pollen germination and tube growth under ambient and high temperature conditions (cowpea – Mutters *et al.*, 1989; tomato - Kuo *et al.*, 1981; lily – Qi and Croes, 1983; maize – Palfi *et al.*, 1981).

Vegetative acclimation, which was imposed before microsporogenesis, reduced pollen germination or fruit-set. This decrease in pollen germination can be attributed to decrease in proline transfer from leaves to anthers and pollen as was observed in tomatoes (Kuo *et al.*, 1981). Vegetative high temperature, which was imposed during microsporogenesis reduced germination dramatically in the sensitive genotype ICGV 92116, confirming the acute sensitivity of pollen mother cell development to high temperature (Gross and Kigel, 1994). Similarly, RA and RHT also had significant effects on pollen germination, and hence fruit-set. The effect of RHT was not much different from VHT, which suggested that most effects on pollen germination were associated with microsporogenesis damage rather than anther dehiscence or impaired pollen germination due to stylar damage.

One interesting observation that requires further investigation is the response of pollen germination to acclimating temperature over the 6d period. Both acclimating treatments (VA and RA) alone or in combination with high temperature (VHT and RHT) show some recovery of germination between 1-2 and 7-8 DAA, compared with other days (3-6 d and 9-12 d), suggesting that

flower buds may have acclimated. Similar observations were recently made by Nakano *et al.* (2000) in common bean.

Temperature level, duration of exposure and genotypic sensitivity determine the extent of heat injury (Li *et al.*, 1991). In the current study, temperature level and duration of exposure were same, so any genotypic differences are an indication of genotypic differences in sensitivity. As suggested by Levitt (1980), plants were exposed to acclimating temperature before subjecting them to high temperature; thus, comparisons in this study reflect true tolerance of the genotypes. Tolerance to high temperature is developmentally dependent (Wardlaw *et al.*, 1980; Abernethy *et al.*, 1989); hence, both vegetative and reproductive stages were evaluated for their tolerance.

In this study, prior exposure to acclimation temperature, either during vegetative or pre-anthesis period, did not improve the performance of the genotypes when exposed subsequently to high temperature. The genotypes neither acquired any heat acclimation potential as described by Li *et al.* (1991) in common bean nor did they behave in a similar way to groundnut genotypes observed by Talwar *et al.* (1999). In groundnut genotypes, ICG 1236, ICGS 44 and ICG 476, Talwar *et al.* (1999) showed that exposure to an acclimation temperature of 35°/30°C prior to heat stress at 50°C, increased the time required to cause 50% damage to the plasmamembrane. Therefore, it was concluded that exposure to acclimating temperature prior to heat stress improves membrane thermostability. The lack of

acclimation in this study indicates that membrane thermostability of genotypes ICGV 92116 and 55-437 was not altered by the imposed treatments.

Instead, the groundnut genotypes in this study behaved in a similar manner to wheat (*Triticum aestivum* L.) genotypes as observed by Stone and Nicolas (1995). Stone and Nicolas (1995) studied acclimation and heat tolerance in two wheat genotypes, Oxley and Erget. They concluded that base or genotypic differences in heat tolerance, determined in the absence of acclimating temperatures, was more important in determining the response to high temperature than acclimating heat potential.

Genotype 55-437 was clearly far more tolerant to high temperature than ICGV 92116. This genotype produced more flowers and set more fruits at high temperature – vegetative or reproductive – than ICGV 92116. The reasons for its greater tolerance in terms of flower production are not obvious from this experiment as only three temperature treatments were used. It is likely that 55-437 has either a higher (warmer) critical temperature for flower production (about 30°C in ICGV 86015) and/or is less sensitive to high temperature (sensitivity of 1.7 flowers plant^{-1} °Cd^{-1} in ICGV 86015). These might be associated with overall greater tolerance to high temperature, as given by RI (Chapter 4).

The cause of the greater fruit-set in 55-437 compared to ICGV 92116 is, however, very clear. Pollen of 55-437 is far more tolerant to high temperature than ICGV 92116. The acclimating temperature of 34°C had almost no effect on

pollen germination, showing that this was close to critical value of 34°C estimated for ICGV 86015. The reasons for greater tolerance of 55-437 over ICGV 92116 might be due to presence of heat tolerant amino acids (e.g. proline) or synthesis of heat shock proteins on exposure to high temperature, which have been discussed in detail in Chapter 4.

5.5 CONCLUSIONS

The results from this study indicate that groundnut genotypes differ in their tolerance to above optimum temperatures. Difference in the genotypes was mainly due to the difference in their base heat tolerance rather than to heat acclimated potential. The temperature tolerance of the genotypes varied with stage of development (vegetative or reproductive) and increases as the crop advances to reproductive phase in the tolerant genotypes. This base heat tolerance can also be observed in specific reproductive processes like pollen germination and pollen tube growth, which are vital for groundnut pod production. Thus, this base heat tolerance of groundnuts can be exploited for breeding genotypes to hot environments.

CHAPTER 6

EFFECTS OF TEMPERATURE AND WATER STRESS ON GROUNDNUT IN A SEMI-ARID TROPIC FIELD

6.1 INTRODUCTION

In the semi-arid environments of the world, which contribute to 90% of global groundnut production, high temperature and water stress often occur together (Nix, 1975; Kramer, 1980). The effects of drought under field situations are well established in groundnut (e.g. Williams *et al.*, 1986; Nageswara Rao *et al.*, 1988; Chapman *et al.*, 1993a). Reports of the effects of increased temperature, both air and soil, in groundnut fields are available in the literature (e.g. Williams *et al.*, 1975b; Sivakumar *et al.*, 1993). However, high temperature studies on groundnut growth and development are confined to controlled environment conditions (e.g. Wheeler *et al.*, 1997; Vara Prasad *et al.*, 1999a, 1999b, 2000).

High temperature studies conducted on groundnut by Vara Prasad *et al.* (1998, 1999a, 1999b, 2000) and in Chapter 3 under controlled environments used a high temperature treatment for a period of 12 h, with temperature changing as a square wave. Such uniform temperature fluctuations do not occur in natural environments. Temperatures under field conditions follow a more sinusoidal pattern, reaching peak during the afternoons (Fig. 6.1). To confirm the findings of studies of high temperature effects on groundnuts conducted in controlled environment, field studies in natural, hot environments are essential. Studies evaluating the effects of both drought and high temperature in groundnut have not been conducted so far under field conditions. Such studies under controlled environment did not result in any definite conclusions (Craufurd *et al.*, 1999).

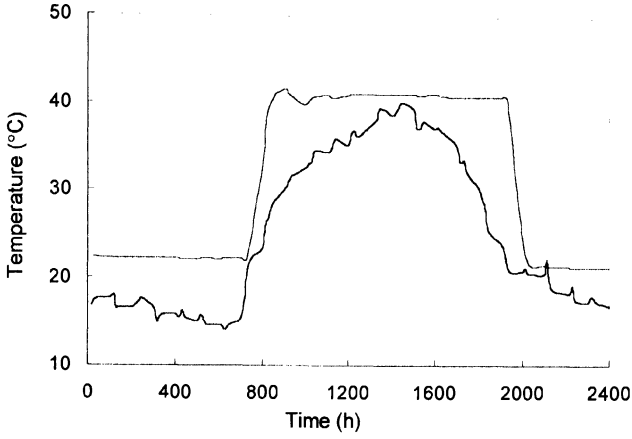


Fig. 6.1 Diurnal temperature cycle under natural (-) hot environment (28-March-1999) at ICRISAT, India, and controlled (-) high temperature treatment (40/22 °C – day/night with 12 h photo-thermoperiod).

An attempt was made in this study to support the conclusions, from the controlled environment study (Chapter 3) for high temperature stress on groundnut yield, and its interaction with drought, under field conditions. The objectives of this study were: (1) to investigate the effects of water stress and high temperature on growth, development and yield of groundnut grown in the semi-arid tropics; (2) to test the possible interaction between water stress and high temperature observed under control environment, on yield and yield components under field conditions.

6.2 MATERIALS AND METHODS

6.2.1 Location

An experiment to study the interaction between high temperature and water stress was conducted in the Indian summer of 1999, with two sowing dates, on an alfisol at the International Crops Research Institute for Semi-Arid Tropics, Patancheru, Hyderabad, India. The ICRISAT is located in semi-arid tropics at an altitude of 545 m ASL, 17°32' N latitude, 78°16' E longitude.

6.2.2 Weather

A mini weather station (Plate 6.1a) was set up to record daily values of temperature and incident solar radiation. Air and soil temperatures were measured using copper-constantan thermocouples. Air temperatures were measured at canopy level, and soil temperatures at 0.10 m depth (i.e. in the podding zone) (Plate 6.1b). Solar radiation received above the crop canopy was measured in each treatment using line quantum sensors (LI-191SB, LI-COR Ltd). Measurements were logged at 10 s intervals and averaged every 15min throughout the crop growth period. Daily weather was also collected from a meteorological observatory located within 500 m of experimental site.

6.2.3 Soil

The soil at the experimental site was a reddish brown alfisol, a member of isohyperthermic family of Udic Rhodustalf. Soil pH was 6.5. Maximum potential rooting depth of soil at the site was 1.2 m. Soil moisture was 20% v/v at field

capacity and 8% v/v at permanent wilting point. These soils are well drained with moderate permeability. Soil characters are described in Table 6.1.

Table 6.1 Physico-chemical properties of the experimental soil (Lithic Rhodustalf) at ICRISAT, Hyderabad, India. (analysed by Rallis India Ltd. Hyderabad).

Particulars	Value	Method of Analysis
	-Mechanical Analysis-	
Fine sand (%)	50	
Coarse Sand	2	International Pipette method (Piper, 1960)
Silt	13	
Clay	34	
	----------Chemical Analysis----------	
pH (1:2 soil water suspension)	7.8	Glass Electrode method (Richards, 1954)
EC (dS m^{-1} at 25°C)	0.07	Solubridge (Richards, 1954)
Organic Matter (%)	0.72	Walkley and Black's modified method (1934)
Available Nitrogen (%)	0.02	Alkaline permanganate method (Subbiah and Asija, 1956)
Available Phosphorous (mg kg^{-1})	60	Olsen's extractant (Olsen *et al.*, 1954)
Available Potassium (mg kg^{-1})	74	Neutral normal Ammonium Acetate (Jackson, 1967)
Exchangeable Calcium (mg kg^{-1})	1680	Neutral normal Ammonium Acetate (Richards, 1954)
	----------Soil Moisture characteristics----------	
Field capacity (% v/v)	20	
Permanent wilting point (% v/v)	8	Gravimetric method (Gardner, 1956)
Available water (% v/v)	12	
Total soil water (mm)	144	

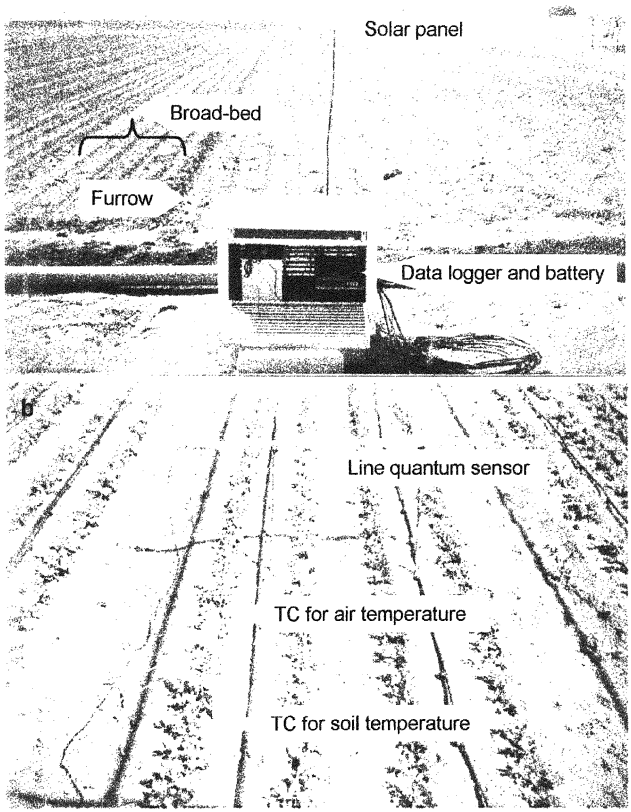


Plate 6.1 Photographs showing (a) broad bed and furrow system with mini - weather station; (b) Line quantum sensor and thermocouples (TC) for measuring air (inside the cup) and soil temperature (0.1 m below soil surface).

6.2.4 Field preparation

The field site was ploughed to a depth of 0.3 m with mould board and disc ploughs 15 d before sowing. The ploughed field was then laid into broad beds (1.2 m wide) and furrows (0.3 m wide), in an East–West direction (Plate 6.1a). The beds were then leveled and compacted. Four furrows at 0.3 m spacing and 0.05 m deep were then opened on the bed surface along the length of the bed. The whole area was then divided into two halves, one for each sowing. Each sowing composed 10 beds of 60 m length. The main irrigation treatments had a bulk bed in between to restrict water seepage between treatments.

6.2.5 Experimental layout details

The treatment and design details are in Table 6.2.

6.2.6 Sowing

Sowing was done on two dates, 21 January and 26 February 1999, to ensure that the crop was exposed to high temperature during the sensitive period of flowering. Seeds were treated with fungicide mixture, Thiram + Captan (3:1), prior to sowing. Seeds of cultivars TMV 2 and ICGS 11 were sown manually, 0.5 m deep and 0.1 m apart in furrows made at 0.3 m spacing on broad beds. An iron chain with tags at 0.1 m spacing was used to ensure that each plot received the required number of plants. Soon after emergence, gaps were filled for ungerminated seeds.

Table 6.2 Details of layout and experimental treatments.

Design		: Split-split plot	
Sowing dates		: Two	S1 – 21 January 1999 S2 – 26 February 1999
Treatments		: Six	
	Main	: Irrigation	IR – Fully irrigated (replacing 100% ETc) WS – Irrigating with 40% of ET_C from flowering to harvest, otherwise fully irrigated
	Sub	: Temperature	T1 – Ambient temperature (sowing1) T2 – High temperature (sowing 1) T3 – Ambient temperature (sowing 2) T4 – High temperature (sowing 2)
	Sub-sub: Genotypes		G1 – TMV 2 G2 – ICGS 11
Replications	: Three		
Plot size	: 9 m long x 1.2 m wide broad bed and furrow		
Spacing	: 0.3 m between rows x 0.1 m between plants		
Harvest	: Sowing 1 – 30 April, 1999 (100 DAS) Sowing 2 – 25 May, 1999 (87 DAS)		

6.2.7 Cultivar description

TMV 2: Released in 1940. Spanish botanical type, a selection from 'Gudhiatham Bunch', a local variety. Widely adapted, well suited for rainy and summer season cultivation in southern India. A leading Spanish variety in the past that still continues to be popular with farmers. Moderately tolerant to water stress and high temperature.

ICGS 11/ICGV 87213: Released in 1986. Spanish botanical type, selection from natural hybrid population of Robut 33-1. Above average tolerance to end of season drought. It is also photoperiod insensitive. Adapted to post-rainy season cultivation in India, performs well in West Africa.

6.2.8 Irrigation treatments

Immediately after sowing, all plots were irrigated using an overhead sprinkler system. A second sprinkler irrigation was given after 7 d to help seedlings to emerge. A drip irrigation system was then installed to provide adequate irrigation to the growing seedlings. The drip irrigation system is shown in Plate 6.3 a and b. Each main plot had a water meter, which was used to monitor the amount of water supplied to plots. Drip pipes were laid in between rows 1 and 2, and between rows 3 and 4 of each plot. Emitters were spaced at 0.6 m on drip pipes; each emitter had water spread over a diameter 0.30 - 0.35 m. The water spread overlapped along and across the rows without leaving any unirrigated patches. The drip emitters were calibrated so that each supplied 10 L hr^{-1} of water to crop

plants. This ensured that all plants in the plot were supplied with equal amount of water. Plots were irrigated at 3 d intervals.

The irrigation treatments were imposed as described here. The fully irrigated plots were replaced with water equal to that lost through crop evapo-transpiration (ET_C). Water stressed plots were irrigated with 40% of that given to fully irrigated plots, from anthesis to harvest. The amount of water supplied to irrigated plot (L) was calculated using:

$$L = \text{Plot area} \times ET_C \quad [6.1]$$

$$ET_C = \text{Evaporation} \times K_C \quad [6.2]$$

where, K_C is the crop coefficient with an average value of 0.8 for groundnut (Doorenbos and Pruitt, 1992) during the reproductive period (K_C during flowering and podding is 0.9 and during maturity is 0.7; Reddy and Reddy, 1985) . The daily ET_C values are presented in Fig. 6.2. The evaporation data was obtained from the weather station at ICRISAT, which is given as:

$$\text{Evaporation} = \text{Open-pan evaporation} \times K_{pan} \quad [6.3]$$

Open-pan evaporation was obtained from an USDA Class A type pan and K_{pan} with a value of 0.7 is the pan coefficient. Water use efficiency was calculated as the ratio of above ground biomass (including pod weight) to the amount of water supplied.

6.2.9 Temperature treatments

Plants were exposed to high temperatures by covering them with plastic tunnels supported by an iron frame, referred to from now on as 'bubbles' (Plate 6.3 a and

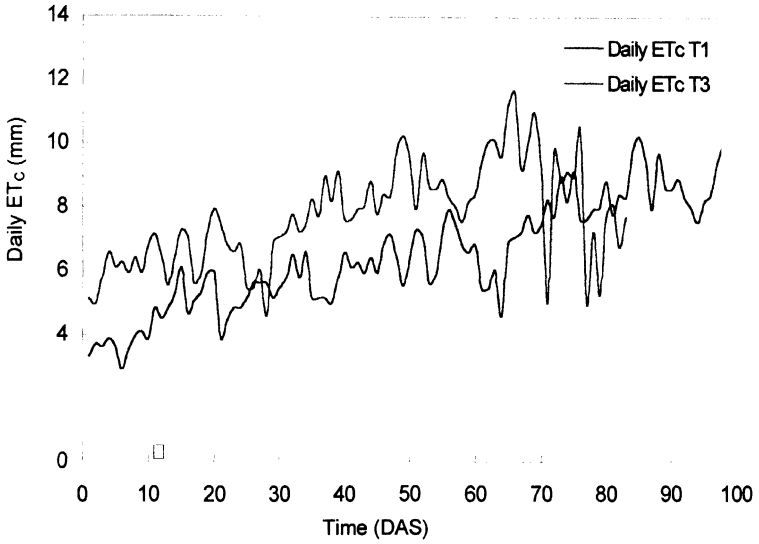


Fig. 6.2 Daily values of ET_C in irrigated treatments between sowing and harvest of the two sowings (T1/T2 and T3/T4). The symbol (□) indicates the start of the drip irrigation treatment.

a

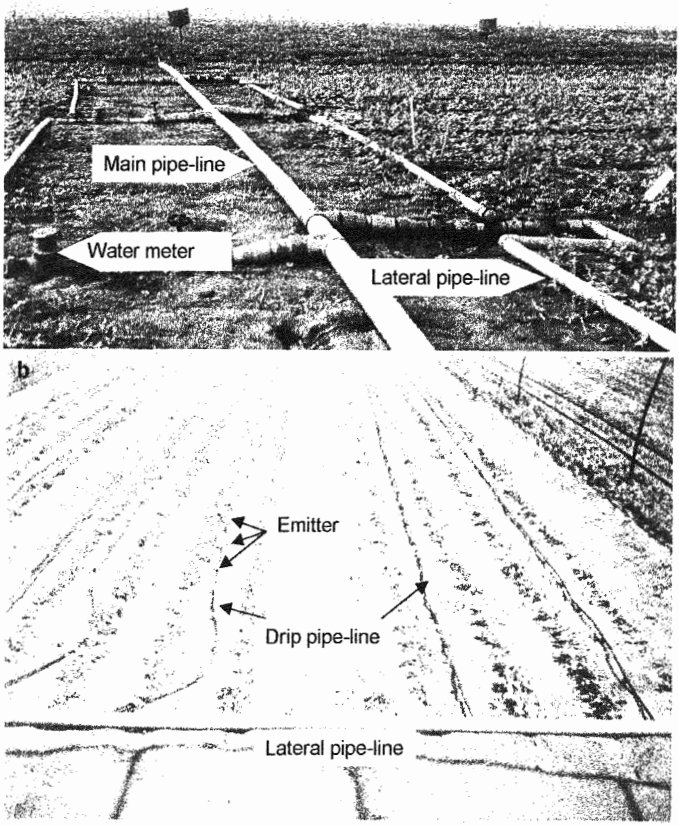


Plate 6.2 Photographs showing (a) components of water measuring devices; (b) drip pipes in the plot with emitters.

b). Plants in the high temperature treatment were covered with bubbles, from flowering to 20 DAF; the most sensitive period for temperature stress (Vara Prasad *et al.*, 1999a). Temperature inside the bubble was controlled so as not to exceed 42-43 °C by opening and closing the flaps of the bubble. This also ensured that humidity did not built up too much in the bubble. The polythene sheet (400 μ thick) used allowed 80% transmittance of light for plants in bubble and the surface was cleaned regularly for any settled dust to maintain transmittance levels.

6.3 OBSERVATIONS

6.3.1 Crop development

The time of the key reproductive stages (R1, R2, R3 and R8 of Boote, 1982) were recorded in each plot. Observations were made daily on 10 plants per plot. The crop was considered to have reached a particular reproductive stage when 50% or more of the plants were at that stage of development.

6.3.2 Growth analysis

Sampling of plants was done once in the vegetative stage, before flowering, and at weekly intervals after imposition of water and temperature stress treatments. An area of 0.6 m^2 (0.5 x 1.2 m) from each plot was sampled at each harvest. A sub-sample of 5 plants was tagged at flowering in each of the harvest areas. Daily flower production was recorded on these plants from flower appearance for a period of 30 d. These plants were also used to determine leaf area and partitioning of dry matter to leaves, stems, and pods. Observations were also

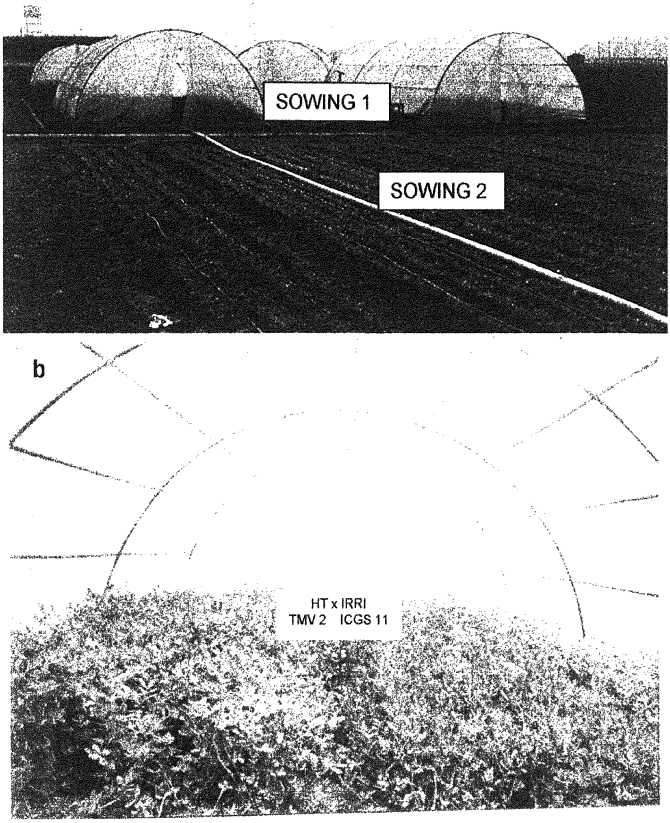


Plate 6.3 Photographs showing (a) layout of bubbles in the field (b) inside of the high temperature x irrigation treatment bubble.

made on plant height, node and leaf number, peg and pod number on plants of the sub-sample. To determine dry weights, plant components of the sub-sample and the remaining part of the large sample was oven dried at 80 °C for 3-4 d and weighed. Total dry matter and pod yields were recorded at harvest maturity in all replications of the experiment using an area of 4 x 1.2 m.

6.3.3 Crop protection

Weeding was done manually, at 30 and 70 DAS to coincide with flowering and pod development, respectively. All experimental plots were relatively free from pest incidence. Slight incidence of thrips (*Megalurothrips usitatus* and *Scirtothrips aurantii*) and spodoptera (*Spodoptera litura*) was noticed in the plots. Thrips were controlled by spraying Dimethoate @200 mL a.i. ha^{-1}. Incidence of spodoptera was controlled by spraying Monocrotophos @ 300 mL a.i. ha^{-1} at 40, 60 and 80 DAS. A minor incidence of bud necrosis was also noticed in water stressed plots.

6.4 STATISTICAL ANALYSIS

All the data were analysed using an analysis of variance procedure (ANOVA) for split-split plot design in GENSTAT 5 (Genstat 5 Committee, 1997). All percentage values were angular transformed before analysis to ensure homogeneity of variances. Pod dry weight was multiplied by 1.65 to account for energy spent to synthesise oil content in the seed (Duncan *et al.*, 1968). Statistical significance was tested by applying F-test at < 0.05, <0.01 and <0.001 level of probability, represented by *, ** and ***, respectively.

6.5 RESULTS

6.5.1 Weather (Temperature and Relative humidity)

A range of temperatures was imposed during flowering by using two sowing dates combined with bubbles. As photoperiod did not vary much at the experimental site (mean 12 h ± 45 min), and the genotypes used were insensitive to photoperiod, results are described in terms of differences in mean temperature between treatments, rather than by sowing dates. Daily maximum and minimum temperatures recorded during the crop period in all the four treatments are presented in Fig 6.3. Temperatures to which different development phases were exposed to in each of the temperature treatments are given in Table 6.3.

A combination of sowing dates and bubbles gave mean temperatures from sowing to maturity of 26.3° (T1), 27.3° (T2), 29.0°(T3) and 29.7°C (T4). The bubbles were capable of raising day temperature by >10°C compared to ambient (Fig. 6.2). During the 20 d high temperature treatment at flowering mean temperatures were 33.8° (T1), 41.6° (T2), 38.7° (T3) and 43.5°C (T4). Increase in soil temperature was also observed with increase in air temperature (Table 6.3). Temperature of soil was highest in the T4 treatment where air temperature was highest.

Average daily relative humidity (RH) in the ambient treatments T1 (sowing 1) and T3 (sowing 2) was 48.4% (SE ± 0.95) and 44.3 (SE ± 0.98), respectively (Fig.6.2). The calculated VPD values were 1.82 and 2.26 kPa in T1 and T3, respectively. It was not possible to record RH in the T2 bubble due to lack of

instruments and therefore VPD could not be estimated in T2. The RH level in T4 during the 20 d period of high temperature averaged to 57% (SE ± 1.12), slightly above that of the ambient T3 treatment. Vapour pressure deficit was therefore slightly lower in T4, 2.06 kPa, than in T3 (2.26 kPa).

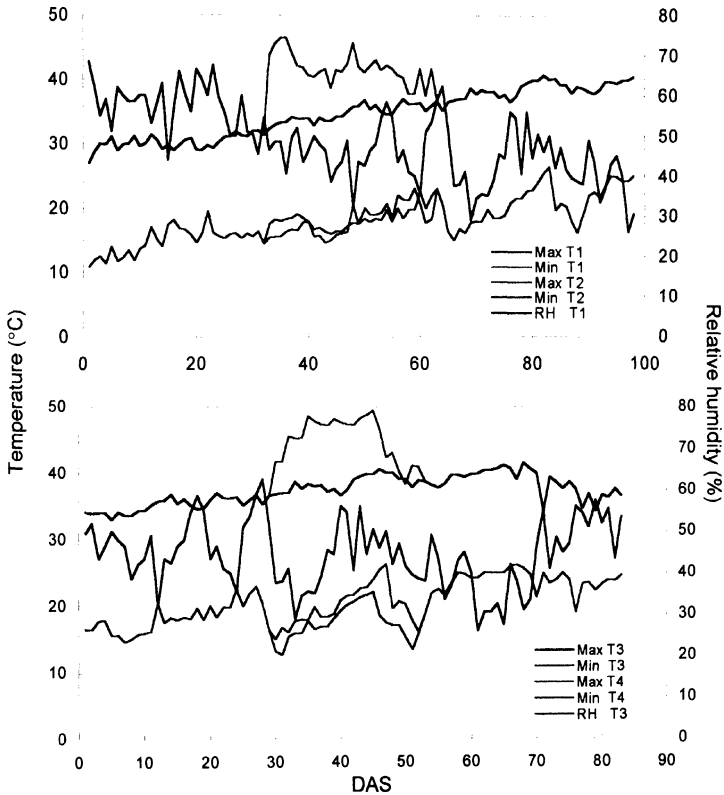


Fig. 6.3 Daily maximum and minimum air temperatures recorded under ambient and high temperature conditions and relative humidity in (a) early and (b) late sown groundnut crop.

Table 6.3 Average maximum (Max), minimum (Min) and mean air temperatures (°C), soil temperatures (°C) and relative humidity (%) recorded during different developmental stages of groundnut in the four temperature treatments to which the crop was exposed in the field.

Developmental Stage	Treatments											
	----------T1----------			----------T2----------			----------T3----------			----------T4----------		
	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
	----------Air temperature (°C)----------											
Sowing – R1	30.2	14.8	22.5	30.7	15.2	23.0	35.2	18.1	26.7	35.3	18.1	26.7
R1 – R3¶	33.9	16.5	25.2	41.6	17.4	29.5	38.7	20.3	29.5	43.5	18.05	30.8
R3 – R8	37.8	20.4	29.1	38.6	20.3	29.5	38.6	23.7	31.2	38.6	23.7	31.2
	----------Soil temperature (°C) ----------											
Sowing – R8	25.8	25.3	25.5	29.4	26.2	27.8	25.9	25.2	25.5	32.3	25.2	30.8
	----------Relative humidity (%)----------											
Sowing to R1	87.5	30.0	58.7	87.5	30.0	58.7	71.3	22.8	47.0	71.3	22.8	47.0
R1 – R3¶	73.3	22.2	47.7	NA	NA	NA	64.4	22.3	43.3	70.3	44.2	57.1
R3 – R8	64.3	23.4	43.8	64.3	23.4	43.8	58.9	26.2	42.5	58.9	26.2	42.5

(Developmental stages: R1=Beginning flower; R3=Beginning pod; R8=Harvest maturity; ¶ = high temperature period; NA –not available)

Due to lower ambient temperature in T1 (sowing 1) bubbles for T2 were kept closed during the greater part of the day to achieve the target temperature of >40°C. This led to a build up of humidity in the bubble near to saturation, which must have reduced VPD. A better control of humidity was achieved in the T4 bubble treatment (sowing 2), keeping the bubble open to reduce the maximum temperature which at times was >48°C. These very high temperatures were achieved because ambient temperatures were much higher at the second sowing (>38°C).

6.5.2 ANOVA

The ANOVA table (Table 6.4) for 2 x 3 x 2 (WS x Temp x Geno) split-split plot analysis with three replications at final harvest shows the main effects and interactions between the treatments. No significant interaction could be recorded at final harvest for temperature and water stress treatments. However, a significant interaction for water stress and temperature was recorded for only peg and pod number in the harvest made immediately after imposing high temperature treatments (i.e. at 54 DAS). Otherwise, only main effects of temperature and water stress, and their interaction with genotypes, could be observed in the various harvests made for growth analysis in the study. Hence, results recorded only at final harvest are presented.

Table 6.4 Analysis of variance with mean square and treatment significance for growth and development parameters recorded at final harvest.

Source	df	VWT	BM	PWT	FLN	PGN	PDN	HI	SLA1	SLA2	WUE
Replicate	2	6269	10997	986	173	85	5	0.0007	146	171	0.03
WS	1	30514*	94008*	17403	108*	356	156*	0.0114	558*	331*	0.05
Residual	2	891	3803	1259	3	114	5	0.0024	10	8	0.008
Temp	2	3768	20915*	16570**	180	375*	3	0.0640***	154	263	0.305*
WS x Temp	2	5276	670	2553	103	214	29	0.0139	437	300	0.044
Residual	8	2176	4516	1179	69	86	18	0.0032	33	169	0.019
Geno	1	681	21776**	14754***	2342***	3589***	668***	0.0648***	4	56	0.070*
WS x Geno	1	657	5487	2344**	289*	23	84*	0.0022*	22	37	0.007
Temp x Geno	2	564	1572	3448***	181*	1171***	175**	0.0225***	265	409	0.002
WS x Temp x Geno	2	1088	2953	457	17	222	5	0.0001	135	50	0.0097
Residual	12	833	1554	218	38	93	17	0.0004	249	133	0.0094

(*, **, *** indicate significance at 0.05, 0.01 and 0.001 levels of probability, respectively; df = degrees of freedom, BM = biomass, FLN = flower number, PGN = peg number, PDN = pod number, PWT = pod weight, VWT = vegetative weight, SLA1 and SLA2 = specific leaf area in sowing 1 and 2, respectively ($cm^2\ g^{-1}$), WUE = water use efficiency,; all weights are $g\ m^{-2}$ and all numbers are per m^2).

6.5.3 Water use and water use efficiency

The cumulative amount of water supplied to irrigated (100% of ET_C) and water stressed (40% of ET_C) treatments is presented in Table 6.5. No monitoring was possible of evaporation in the high temperature treatments T2 (sowing1) and T4 (sowing 2). Hence, similar amounts were supplied to ambient (T1 and T3) and high temperature (T2 and T4) treatments irrespective of irrigation treatment. Amount of irrigation given was higher in T3 and T4 treatments due to greater ET demand associated with the increase in ambient temperature and VPD in the second sowing.

Table 6.5 Cumulative amounts of irrigation (mm) supplied to irrigated (IR-100% of ET_C) and water stressed (WS – 40% of ET_C) plots during different stages of development.

Development stage	T1 and T2		T3 and T4	
	IR	WS	IR	WS
Sowing – R1	121	121	204	204
R1 – R3	98	43	201	89
R3 – R8	355	183	234	91

Water stress treatments did not influence WUE (above ground biomass/total water added). Water use efficiency was significantly affected by main effects of temperature and cultivar. Genotype ICGS 11 recorded significantly ($p<0.01$) higher WUE of 0.74 g L^{-1} compared to 0.65 g L^{-1} in TMV 2.

Sowing date and temperature treatments significantly affected WUE (Table 6.6). At ambient temperature, WUE was higher in T1 (sowing 1) than T3 (sowing 2), and this was associated in part with a lower VPD at T1. The highest WUE, 1.21 g m^{-2} L^{-1}, was recorded in T2, and both high temperature treatments, T2 and T4, increased WUE compared to their respective ambient controls.

Water use efficiency (WUE) is strongly affected by VPD, which was lower at sowing 1 (T1) than sowing 2 (T3). The normalised values of WUE for T1 and T3 were 1.6 and 1.3 g kPa L^{-1}, respectively. The higher WUE at sowing 1 was probably due to cooler mean temperatures (Table 6.3). The higher WUE in T4 compared to T3 is accounted for by the lower VPD in T4, which in turn is due to the high RH in the bubble. Although RH was not measured in T2, RH was very high in the bubble, and the high WUE in T2 is undoubtedly due to a lower VPD. Accordingly, T2 has been excluded from further analysis.

Table. 6.6 Effect of temperature treatments on WUE (g L^{-1}) and VPD (kPa) and normalised WUE (WUE x VPD (g kPa L^{-1}).

Temperature treatments	WUE	VPD	WUE normalised For VPD
T1	0.88	1.82	1.6
T2	1.21	NA	NA
T3	0.58	2.26	1.3
T4	0.64	2.06	1.3
SED	0.055***		

(NA – not available)

6.5.4 Effects of temperature x water stress interaction

Table 6.7 shows the interaction effects for temperature and water stress treatments. The effects of temperature and water stress interaction were apparent only in the harvests made immediately after ending the 20 d high temperature treatment; this interaction disappeared as the crop reached maturity. The interaction was significant (<0.05) between T3 and T4 for both peg and pod number at 54 DAS. High temperature imposed in the irrigated treatment (IR) decreased the peg (50%) or pod (54%) number. Water stress treatment (WS) also reduced peg (68%) and pod (72%) number in ambient temperature conditions. However, a combination of high temperature (T4) and water stress (WS) increased peg, and in particular pod, number relative to WS or T4. In general water stress effects were more severe than high temperature effects.

Table 6.7 Effects of temperature (mean of 20 d high temperature) and water stress treatments on peg and pod number (plant^{-1}) recorded in the harvest made immediately after the withdrawal of high temperature treatments.

Water stress treatments	Temperature treatments	
	T3 (29°C)	T4 (31°C)
	Peg number	
Irri	15.81	7.96
WS	6.60	8.09
SED	2.35*	
	Pod number	
Irri	3.72	1.74
WS	1.03	2.84
SED	0.76*	

6.5.5 Effects of water stress and its interaction with genotypes

6.5.5.1 Specific leaf area

Water stress treatments altered the specific leaf area of plants exposed to water stress treatments. When both sowings were analysed together, there was no water stress x sowing interaction nor the main effects of water stress or sowing significant. However, when each sowing was analysed separately, then differences between water stress treatments were apparent ($p<0.05$) (Fig. 6.4). Water stress (40% ET_C) increased SLA in sowing 1, while it decreased SLA in sowing 2.

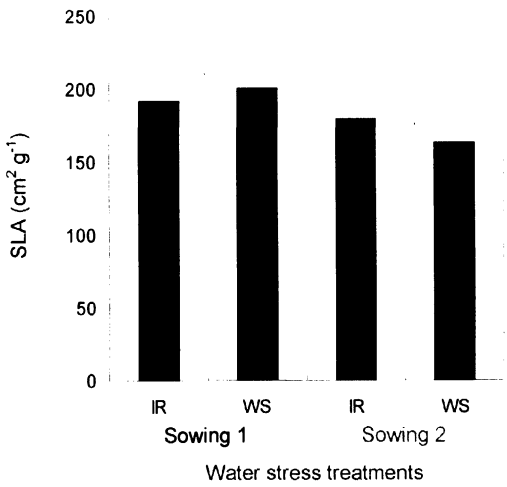


Fig. 6.4 Specific leaf area (SLA) values recorded in water stress treatments (IR - 100% ET_C and WS - 40% ET_C) in the two sowings. (SED: Sowing 1 – 1.14*; Sowing 2 – 1.28*)

6.5.5.2 Biomass and pod yield

Seasonal time course of biomass and pod weight in T1 is shown in Fig. 6.5. There was no immediate effect on biomass or pod weights of the 20 d high temperature period. However, water stress treatment decreased biomass and pod weight throughout the stress period.

Main effects of water stress were recorded only for biomass due to significant ($p<0.05$) reduction in vegetative and pod weight. Vegetative (283.9 g m^{-2}) and pod weight (120.2 g m^{-2}) in irrigated treatments (100% ET_C) were reduced by 20 and 37%, respectively, due to water stress treatment (40% ET_C).

Cultivars differed in their response to water stress treatments (Table 6.8). The interactions persisted until the final harvest. Cultivar ICGS 11 recorded significantly ($p<0.05$) higher values for flower number (40%), pod number (50%), pod yield (37%) and harvest index (31%) than TMV 2 under irrigated conditions (100% ET_C). When the genotypes were supplied with 40% ET_C, the differences for tolerance to water stress were clear between the genotypes. Flower number, biomass, pod yield and harvest index decreased by 14, 31, 42 and 14% in ICGS 11 and by 0, 23, 28 and 4% in TMV 2, respectively, compared to those obtained in the irrigated treatment. There was no effect of water stress treatments or its interaction with genotypes on peg and pod number and pod set.

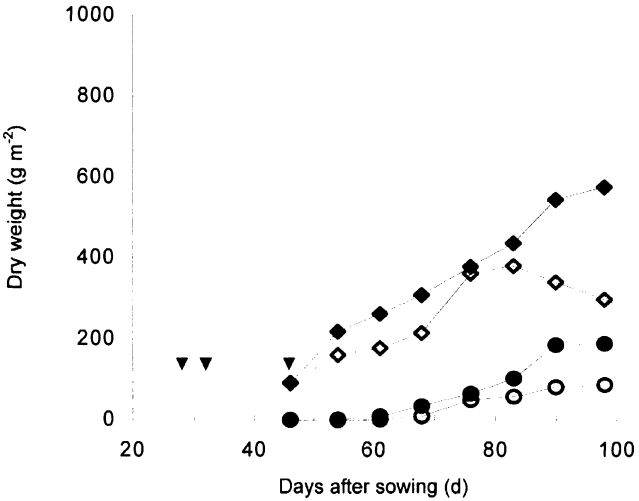


Fig. 6.5 Seasonal timecourse of biomass (diamond) and pod weight (circle) recorded in water stress treatments, Irri (100% ET_C - closed) and WS (40% ET_C - open) in T1 treatment; ▼indicates start and end of high temperature treatment, while ▼indicates start of water stress (WS - 40% ET_C) treatment.

Table 6.8 Interaction between genotype and water stress treatments for flower number (plant^{-1}) at 30 DAA, pod number (plant^{-1}), pod yield (g m^{-2}) and harvest index as observed at final harvest.

Water stress	Cultivar	
	TMV 2	ICGS 11
----------Flower number----------		
Irri	32	53
WS	34	44
SED	2.1*	
----------Pod number----------		
Irri	12	24
WS	11	17
SED	1.5*	
----------Pod yield----------		
Irri	91.9	148.5
WS	66.1	88.4
SED	6.4**	
----------Harvest index----------		
Irri	0.23	0.33
WS	0.21	0.28
SED	0.017*	

6.5.6 Effects of temperature and its interaction with genotypes

Main effects of temperature were significant for biomass (Fig. 6.6). High temperature decreased biomass in T3 and T4 by 21 and 12%, respectively, compared to T1. The smaller decrease in biomass in T4 compared to T3 can be attributed to lower VPD in T4. Similar trend was also recorded for vegetative weight (data not presented).

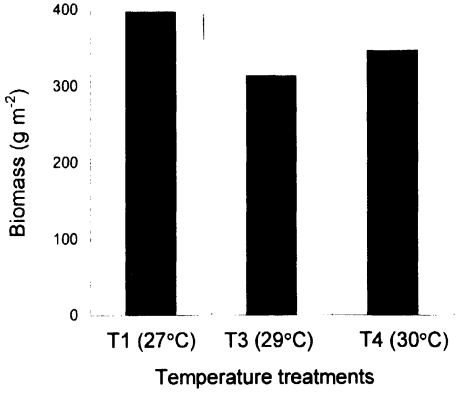


Fig. 6.6 Effect of temperature treatments on final biomass averaged across different water stress treatments and genotypes. Vertical bar indicates SED.

The interaction of temperature treatments with water stress disappeared with advance in crop age, but temperature interactions with cultivar persisted until final harvest. A temperature x cultivar interaction was recorded for flower number, pod number, pod yield and harvest index (Table 6.9).

Table 6.9 Interaction between genotype and temperature treatments for flower number (plant^{-1}) at 30 DAA, pod number (plant^{-1}), pod yield (g m^{-2}) and harvest index as observed at final harvest.

Cultivar	Mean temperature treatments (°C) T1(27)	T3 (29)	T4 (30)	SED
	----------Flower number-------			
TMV 2	35	35	28	4.2*
ICGS 11	42	55	50	
	----------Pod number----------			
TMV 2	16	10	10	2.4**
ICGS 11	15	24	22	
	---------Pod yield----------			
TMV 2	140.0	51.0	42.8	15.26***
ICGS 11	142.2	103.8	109.4	
	---------Harvest index---------			
TMV 2	0.36	0.18	0.14	0.024***
ICGS 11	0.34	0.29	0.28	

Of the two cultivars, ICGS 11 was more tolerant to high temperature. In both cultivars, a decrease in pod yield and HI was recorded under high temperature treatments, but the decrease was significantly less in ICGS 11 compared to the decrease in TMV 2. Cultivar ICGS 11 maintained a high pod yield and high HI under high temperature treatments (T3 and T4). On the other hand, a severe decrease in pod yield and HI were recorded in TMV 2. The higher pod yield and HI in ICGS 11 can be attributed to greater flower fruit-set (i.e. ratio of pod to

flower number) and pod number. In contrast, in TMV 2, reduction in flower number and fruit set was recorded, and so pod number was decreased on exposure to high temperature.

6.6 DISCUSSION

Studies conducted so far to identify temperature x water stress interactions (Craufurd *et al.*, 1999) or to screen genotypes for heat tolerance, have been conducted mainly in controlled environments (Vara Prasad *et al.*, 1999a, 1999b; 2000; Wheeler *et al.*, 1997). Under these conditions, the temperature increase follows a square wave pattern (Fig 6.1). Hence, an interaction between temperature and water stress occurs on plant growth during the entire 12 h of photo-thermo period, providing a longer period for the interaction to influence the growth and development of the crop plant under study. However, under field conditions, increase in day temperature follows a more or less sinusoidal pattern (Fig 6.1), and high air temperature effects on plant in field occur for a short duration of only 3-4 h. Furthermore, the temperature of plant canopy in SAT regions can be higher than that in controlled environment under similar air temperatures due to associated radiative heating (Guilioni *et al.*, 2000). Hence, the interaction between the stress events that occur under controlled environment might be different from those occurring in the field. If true, this would have important implications for using controlled environment facilities for screening for water and temperature stress.

Total water added or used (ET_C) was slightly higher in the second (639 mm) than first sowing (574 mm) and this was due to higher VPD associated with increasing mean temperatures. Water use efficiency (WUE), derived as the ratio of total above ground biomass to total water added and corrected for differences in VPD, was lower in the second than in the first sowing (1.3 cf 1.6 g kPa L^{-1}). However, water stress had no effects on WUE. The values of WUE (as opposed to transpiration use efficiency) are at the lower end of values found in other field or controlled environment studies (e.g. 2 to 5 g kPa L^{-1}; Mathews *et al.*, 1988; Ong, 1987; Wright *et al.*, 1996). Results in this study are from a groundnut crop grown in the harsh climate of the Indian SAT summer, when day (37°-39°C) and night (20°-24°C) temperatures are high; in contrast comparative studies are from kharif or rabi crop in India or controlled environments where mean temperatures are close to 25°C (Azam Ali *et al.*, 1989; Craufurd *et al.*, 1999; Wright *et al.*, 1996).

The lack of significant difference for WUE between IR (100% ET_C) and WS (40% ET_C) treatments shows that a decrease in biomass resulted from a reduced water supply. It is widely accepted that actively transpiring plants keep their stomata open through which CO_2 enters the plant that is converted into biomass by the photosynthetic apparatus (Hsiao, 1973). Any reduction in water supply to groundnut plants would force the plants to close their stomata to conserve water through reduction in T (Azam Ali, 1984; Patil and Patil, 1993). The closure of stomata would impede the passage of CO_2 and result in a reduction of CO_2 assimilation rate, thus lowering the biomass. Hence, a reduction of T in WS

treatment if identified, would answer the cause for reduction in biomass due to WS in this study.

In order to account for decrease in biomass under water stress, specific leaf area and VPD (Table 6.10) were used with eqs. 3.2 to 3.6 (see Chapter 3) to estimate transpiration efficiency (TE) and then transpiration (T), and hence proportion of ET_C used as T or lost as soil evaporation (E_S). The above ground biomass including pod dry weight, was used in estimating TE and T. The estimated TE and T values are presented in Table 6.10.

Table 6.10 Observed specific leaf area (SLA) and vapour pressure deficit (VPD) in water stress treatments, carbon isotope discrimination (Δ = 0.03SLA + 14), normalised TE (k = - 0.53Δ + 14.4) transpiration efficiency (TE = k/VPD), transpiration from sowing to harvest (T) derived from SLA values using the equations described by Wright *et al.* (1996).

Water stress treatment	SLA ($cm^2\ g^{-1}$)	Δ (ratio)	K (g kPa L^{-1})	VPD (kPa)	TE (g L^{-1})	T (mm)
----------Sowing 1----------						
IR	192	19.76	3.92	1.82	2.16	209
WS	201	20.04	3.78	1.82	2.08	116
SED	1.1*					
----------Sowing 2----------						
IR	180	19.41	4.11	2.26	1.82	165
WS	164	18.91	4.37	2.26	1.94	99
SED	1.3*					

The crop simulation model for groundnut, PNUTGRO (see Chapter 7) was also used to approximately estimate the soil water balance and T/E_S ratio (Fig. 6.7). The weather, soil and irrigation data during the growth period, and genetic

coefficients measured in the field study were used to simulate the water balance. Model predictions indicate that the crop was actively transpiring untill harvest in the IR treatment. In WS treatment transpiration started to fall below that of the IR treatment at around 60 DAS. This occurred as soil moisture started to drop below the critical level of 40% ASM for groundnut (Wright and Nageswara Rao, 1994) at this stage (Fig. 6.10).

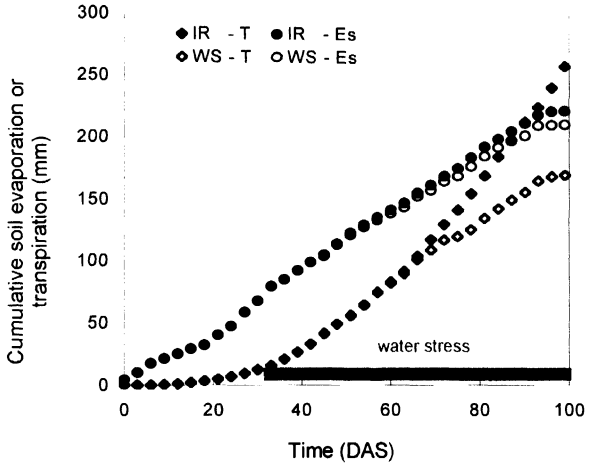


Fig. 6.7 Simulated values (using PNUTGRO) of cumulative soil evaporation (E_S) and transpiration (T) values in irrigated (IR, supplied with 100% ET_C) and water stressed (WS, supplied with 40% of ET_C from flowering) treatments in sowing 1 from sowing to harvest.

The values of TE were similar in IR and WS treatments at each sowing, but were slightly lower at sowing 2 than in sowing 1. Data in Table 6.10 suggests that TE is conservative over a wide range of stress conditions once any differences in VPD are considered. The TE values estimated from SLA in the field experiment are low (1.9 to 2.2 g L^{-1}) when compared to the values obtained in controlled

environment experiment in Chapter 3 (3.2 to 4.2 g L^{-1}) and lower compared to those obtained for groundnut crop in kharif and rabi seasons of India and in Australia (~ 3.0 g L^{-1}) by Wright *et al.*, (1996). These values are, however, comparable to those obtained by Hubick *et al.* (1986) when groundnut studies were conducted in glasshouse at a VPD of 2.2 kPa. Values similar to those reported here were also obtained by Azam Ali *et al.* (1989) at VPD of 2.1 kPa in drying soil and Mathews *et al.* (1988) at a VPD of 1.9 kPa in dry season with occasional irrigation. These differences in TE probably largely reflect differences in VPD since the values of *k* in the controlled environment and field were similar, 3.5 to 4.0 g kPa L^{-1}.

Given that values of TE were similar in IR / WS and temperature treatments (no significant differences in SLA or normalised WUE (Table 6.6)), variation in biomass was therefore due mainly to variation in T. The estimated values of T are also given in Table 6.10, and confirm that both water stress and later sowing reduced T and therefore biomass. The model also shows that E_S remains nearly constant in both IR and WS treatments, but T is reduced in WS treatment (Fig. 6.7). When T is expressed as a proportion of ET_C, T accounted for 36 and 33% of ET_C in the IR and WS treatments, respectively, at sowing 1, and 25 and 25%, respectively, at sowing 2 (Fig. 6.8). Therefore, more water is lost through E_S in sowing 2.

Values of T were also estimated using the PNUTGRO model (T_{sim}) (Boote *et al.*, 1999) and compared with ET_C, and T values estimated from SLA (T_{sla}) in Fig. 6.8. Values of T estimated by PNUTGRO are greater than those estimated from

SLA, but across sowing dates and treatments the trends were similar. The model predicted higher T of 45 and 35%, similar in both IR and WS treatments, in sowing 1 and sowing 2, respectively. The higher value of T from PNUTGRO is due to the higher biomass predicted by the model in environments with high temperature (details in Chapter 7). The current experiment was conducted in summer of 1999 when temperatures averaged around 37 °C.

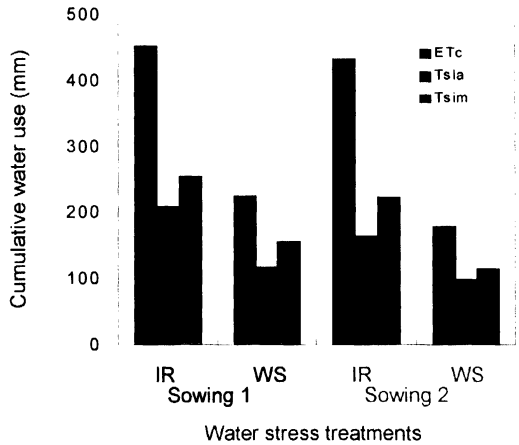


Fig.6.8 Amount of water supplied to the crop (ET_C) and cumulative transpiration values derived from SLA (T_{SLA}) and simulated by PNUTGRO (T_{SIM}) in irrigated (IR – 100% ET_C) and water stressed (WS - 40% ET_C) treatments, from sowing to harvest, in sowing 1 and sowing 2.

A decrease of 20% in total ET in water stress treatments compared to fully irrigated treatments due to a decrease in T was recorded by Pallas *et al.* (1979). At a similar plant density to the current study, Azam-Ali *et al.* (1989), in a field study during kharif season (June sowing) at ICRISAT in India, recorded a transpiration of only 150 mm from sowing to 97 DAS. In the present study, T was

209 mm and 116 mm in IR and WS treatments, respectively, in sowing 1; and was 165 and 99 mm in IR and WS treatments, respectively, in sowing 2. This can be attributed to higher radiation and temperature recorded in the current study along with a lower VPD, causing greater water loss through evaporation. Studies by Azam-Ali *et al.* (1989) and Mathews *et al.* (1988) conclude that increase in radiation increases T as it is essential to maintain canopy temperature at or below ambient temperature. A decrease in transpiration as recorded under water stress in this study was also reported by Balasubramanian and Maheswari (1990) and Patil and Patil (1993). These studies thus confirm that water stress reduces the transpiration rate and inturn decreases total biomass accumulated.

Temperature increase across the treatments, T1 to T4, (Table 6.3) was achieved by using plastic bubbles in the field. Humidity was controlled in these bubbles by opening the bubble doors for brief periods during the day; nonetheless, an increase of humidity in these bubbles did occur, particularly at sowing 1 (i.e. T2). Lee *et al.* (1972) recorded that an increase in humidity from 50 to 95% increased the flower and peg number, and vegetative weight. Similar observations were made in this study, notably in T2 where the RH was near saturation compared with 48% under ambient conditions. The use of bubbles resulted in clear temperature differences across treatments. These bubbles can thus be used in the field to screen groundnut genotypes for high temperature tolerance, as humidity control can be achieved with experience in using the bubbles (T2 vs. T4). The effects of temperature and water stress on components of groundnut recorded at final harvest are summarised in the flow diagram (Fig. 6.9).

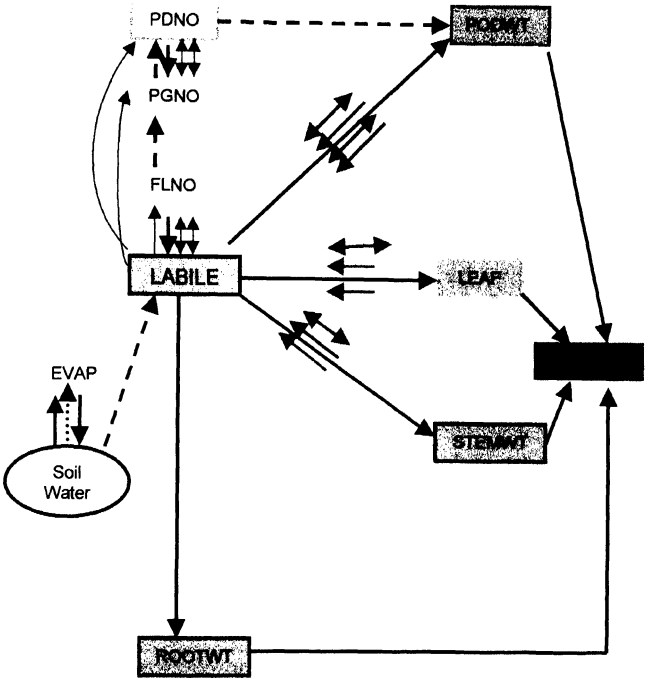


Fig. 6.9 Summary of the results of high temperature and water stress effects on growth and development of groundnut in SAT. (Thick arrows = main routes for assimilate translocation; Thin black arrows = routes for minor use of assimilates; broken arrow = information flow; red arrow = temperature effects; blue arrow = water stress effects; red and green arrow = interaction of temperature and genotype; blue and green arrow = interaction of water stress and genotype; Labile = current and stored assimilate pool; WT = weight; PDNO =pod number; PGNO = peg number; FLNO = flower number). Direction of red/blue arrows opposite to assimilate route indicates negative effects.

The field study also confirms the observations made under controlled environment studies (Chapter 3) that the interaction for temperature and moisture stress is transient and disappears with release of high temperature stress treatment. Thus, an interaction between temperature and water stress treatments was recorded in the harvests made immediately after the withdrawal of high temperature treatment (T4). The interaction between water and temperature stress was significant only for peg and pod number. This interaction is due to the sensitivity of the reproductive processes such as pollen germination and fertilisation to high temperature. In controlled environment with a maximum temperature of 37°C for 10 d, a decrease in pod number of 43% was recorded at 50 DAS (Chapter 3). On the other hand, in the field experiment a temperature of 43.5°C was imposed for 20 d, resulting in a reduction of only 46% in pod numbers. This lesser decrease in pod number can be attributed to the greater tolerance to high temperature of the genotypes used in the field (ICGS 11 and TMV 2) study compared to those in controlled environment (ICGV 86015 and ICG 796). Observations made on membrane thermostability and cardinal temperatures for pollen germination and tube growth (Chapter 4) show that genotypes tested in field were more tolerant than those tested in controlled environment.

The reasons for the existence or disappearance of the interaction between water and temperature can be attributed to the moisture level at that particular stage of crop growth. In the controlled environment study the interaction with high temperature occurred at a soil moisture content in the water stress treatment of

60% ASM. The ASM at the end of the high temperature treatment in the field experiment, i.e. at 50 DAS was also estimated to be about 60% (Table 6.11 and Fig. 6.10). A simple water balance was used to estimate ASM – assuming that water loss was equal to ET_C and this is detailed in Table 6.11.

Table 6.11 Simple water balance for sowing 1 during the water stress and high temperature treatment.

Soil depth	=	1.2 m
FC	=	20% v/v
PWP	=	8% v/v
Percentage water available	=	12% v/v
Total soil water available (100% ASM)	=	(12/100) x 1.2 x 1000 = 144 mm
Water lost from soil during HT treatment (ET_C)	=	98 mm
Water added to WS x HT during HT treatment	=	43 mm
Total soil water lost	=	98 - 43 = 55 mm
Soil moisture percentage when 55 mm is lost	=	((144 - 55) / 144) x 100 = 61.8%

Similarly, the crop model PNUTGRO was used to estimate the ASM and the simulated value in irrigation treatments at sowing 1 are given in Fig. 6.10. The ASM averaged 70% from sowing to harvest in IR treatment, while in WS treatment ASM declined from 60 % at 30 DAS to about 20% at 100 DAS (averaged 30%). The model PNUTGRO thus predicts a lower ASM, averaged 70%, in the irrigated treatment, eventhough 100% of ET_C was replaced. This can be attributed to the drainage losses predicted by the model. PNUTGRO predicts

a 30% loss of water applied through drainage in both IR and WS treatments, although drip system was used to irrigate the crop. In drip system of irrigation deep percolation (drainage) and surface runoff loss is non-existent (Reddy and Reddy, 1985). Hence, the model fails to account for benefits of the drip system and thus predicts lower soil moisture.

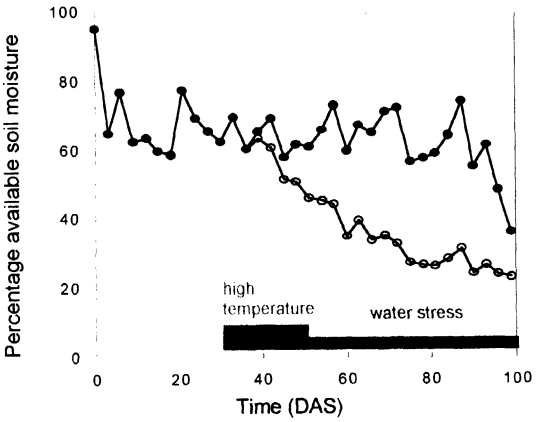


Fig. 6.10 Simulated values (using PNUTGRO) of percentage soil moisture in irrigated (■ supplied with 100% ET_C) and water stressed (□ supplied with 40% of ET_C from flowering) treatments in sowing 1 from sowing to harvest.

If the loss in drainage is added to the ASM predicted by the crop model, the simulations also confirm the soil water balance calculations (Table 6.11) shown above that the soil was around 60% ASM at the end of high temperature treatment. The ASM would average 100% from sowing to harvest in irrigated plots. In case of water stressed plots, ASM would average 40% during the stress

period. Therefore at the end of the high temperature treatment, comparable soil water conditions resulted in controlled environment and field experiments, and comparable interaction between water stress and high temperature were found.

Controlled environment and field studies also suggest that when soil moisture is around or less than 40% ASM, critical for groundnut (Wright and Nageswara Rao, 1994). At 40% ASM, water stress dominated the stress effects and no interaction between water stress and high temperature could be identified. As water is a reactant or substrate for many reactions in plant (Kramer and Boyer, 1995) and the rate at which these reactions occur is affected by temperature (Johnson and Thornley, 1985). Thus when water stress goes below 40% ASM, available substrate is limited, and hence role of temperature on the reaction rates in plant is reduced.

The results from this field study clearly show that both temperature and water stress decrease pod yields in groundnut, but the cultivars used in this study differed in their responses to temperature and water stress. Temperature moderately reduced total biomass or vegetative weight (leaf+stem). In contrast, a severe decrease in pod yield was recorded due to high temperature. However, under water stress conditions, a greater decrease in biomass and vegetative yield occurred along with a decrease in pod yield. This provides evidence to suggest that crop plants react differently to environmental stresses and adopt different strategies to overcome the stress events occurring at a particular location.

Pod yield decrease under water stress conditions can be attributed to a decreased source (vegetative weight), and in one cultivar to a slight decrease in partitioning. Such decrease in vegetative weight has been recorded in many experiments (Wright *et al.*, 1991; Sarma and Sivakumar, 1989, 1990). There exists evidence in literature for this decrease in pod yield under water stress conditions (Nageswara Rao *et al.*, 1988; Ravindra *et al.*, 1990; Williams *et al.*, 1986). Thus, under water stress conditions pod yield is source limited. Decrease in partitioning was also recorded in earlier studies by Greenberg *et al.* (1992).

Genotypes used in this study differed in their response and tolerance to temperature treatments imposed (Fig. 6.9). Genotypes did not differ in their vegetative weight, indicating that source was not limiting in them. Thus processes like photosynthesis or respiration, responsible for source, are not much altered in them. In contrast, pod yield was reduced in both the genotypes.

A greater reduction in pod yield of >70% occurred in TMV 2, while it was only around 23% in ICGS 11. This indicates that ICGS 11 is more tolerant to high temperature than TMV 2. The greater tolerance of ICGS 11 to high temperature can be attributed to maintenance of a significantly higher partitioning under increasing temperature conditions. This higher partitioning is due to greater sink strength in ICGS 11 than in TMV 2. Such genotypic differences for reduction in pod yield when exposed to high temperature were recorded earlier by Talwar *et al.* (1999), Vara Prasad *et al.* (1999, 2000) and Wheeler *et al.* (1997). In a screening study conducted in 1991 in Sahelian region of Africa, Ntare *et al.*

(2001) demonstrated that groundnut genotypes significantly differ in their pod yields in hot environments due to the effects on partitioning.

Under water stress conditions, a greater reduction in vegetative weight and pod yield occurred in ICGS 11 than in TMV 2. Although the reductions were greater in ICGS 11 under water stress, this genotype had higher vegetative and pod yield under irrigated conditions. This is due to greater accumulation of assimilates and higher partitioning of these assimilates to pod yield (Table 6.8). Under water stress only a slight decrease in flower number occurred in ICGS 11, which did not significantly influence the peg and pod number. No such decrease in flower number occurred in TMV 2. In addition, the genotype ICGS 11 had a higher WUE when compared to TMV 2. This allowed the genotype to accumulate greater biomass even under water stress conditions. Hence, genotype ICGS 11 was tolerant to both high temperature and water stress conditions over TMV 2.

6.7 CONCLUSIONS

It can be inferred from this study that genotypes that are tolerant to water stress are also tolerant to high temperature under field conditions. Mechanisms that a genotype adopts to overcome stresses differ. However, genotypes with ability to establish greater biomass and with a significantly greater partitioning of biomass to pod yield would be suitable for sustaining higher yields in SAT areas with high temperature and water stress. Genotypes with greater WUE are also more useful for the SAT. Thus screening of groundnut genotypes for both temperature and water stress tolerance in field conditions are essential before recommending

them for SAT and before using them for further breeding of new genotypes to these stresses. Controlled environments can be used for screening genotypes to high temperature for specific processes and experiments under field conditions needs to be adopted to identify the various mechanisms for tolerance involved.

CHAPTER 7

MODELLING THE EFFECTS OF WATER STRESS AND HIGH TEMPERATURE IN GROUNDNUT USING PNUTGRO

7.1 INTRODUCTION

A crop or genotype is adapted for maximum output (economic yield) at a given location. Introduction of this crop or genotype into a new environment requires selection of optimum management practices for that location or field. Environment plays a major role in determining the new optimum management practices as it alters the pattern and rate of development and growth in the new location. The more the environment deviates form the optimum conditions for a crop or genotype, the greater are the changes required in management practices (e.g. fertiliser, irrigation) to reap maximum output in a given location.

The main weather constraints for crop production in the tropics and SAT are low (<700mm) and uneven distribution (long dry periods) of rainfall and occurrence of high temperatures (>34°C) during the crop growth period. For future climates, predictions for SAT regions indicate an increase in temperature with a warming of 1.5° to 5.8°C in the 21st century (IPCC, 2000). This warming may increase the temperatures to >34°C during the sensitive stages of groundnut cultivation, i.e. flowering and pod development, in the SAT. Experimentation under field conditions to test these predicted temperatures poses problems that require a lot of specialist equipment and resources. To overcome the limitations, crop models can be used as surrogates for field experimentation.

Crop models are developed in a laboratory or research station from a limited number of experimental data sets. Although crop models seek to quantify the effects of environment on crop processes, in reality they are often location

specific or site specific, and work effectively only in those locations for which they have been calibrated (de Wit and Van Kulen. 1987; Hunt and Boote, 1998). Calibration for a given location can correct for multiple and hidden sources of error (Rastetter *et al.*, 1992). Thus, crop models require a certain amount of calibration before they can be used for yield prediction or forecasting at a new location. Through calibration, the genetic coefficients are modified to account for the genotype x environment interaction. Many current models lack the built in ability for genotype x environment interaction that might make calibration a simpler process (Tsuji *et al.*, 1994).

Of the various models developed for groundnut, CROPGRO-Peanut (PNUTGRO) is the most widely used and validated for various systems of groundnut cultivation (Singh *et al.*, 1994a; 1994b; Boote *et al.*, 1998, 1999; Kaur and Hundall, 1999). The PNUTGRO model is process-oriented and considers crop development, crop carbon balance, crop and soil - N balance, and soil water balance. Temperature effects on growth and development are also simulated by this model. The main constraint in this crop model is its inability to account for pest and disease damage on crop growth and development, and on final crop yield (Boote *et al.*, 1986). All the variation unaccounted in PNUTGRO has been assigned to a single factor - SLPF (soil fertility factor), this factor considers that the site to site variations are mainly due to differences in fertility (Boote *et al.*, 1998).

Crop models can also be used for precision forecasting of crop yields, identifying research gaps and making policy decisions (Boote *et al.*, 1998). Predictions for larger areas (e.g. regional or national) compared to predictions of small homogenous plots need to consider greater variation in weather, soil and management practices. As the model cannot account for G x E, a factor or two in crop models which can be changed easily and are characteristic of a given region in order to give reliable yield prediction need to be identified.

The following simulation exercise was designed to (i) calibrate the PNUTGRO model for five locations in India; and (ii) evaluate PNUTGRO for its ability to predict the effects of high temperature and water stress observed in the field study reported in Chapter 6.

7.2 MATERIALS AND METHODS

7.2.1 PNUTGRO

The PNUTGRO model has been described in several publications (Boote *et al.*, 1986, 1992; Boote and Jones, 1988) and widely evaluated for growth and development under conditions without biotic stress (Singh *et al.*, 1994a; 1994b; Kaur and Hundal, 1999). An overall description of the model and its ability to predict crop growth and development has also been presented in Chapter 2. Hence, only the temperature responses in the model are described here.

7.2.2 Temperature responses in PNUTGRO

In PNUTGRO, vegetative processes that are sensitive to temperature include the rate of germination and emergence, rate of vegetative node formation, duration of vegetative growth, photosynthesis, maintenance respiration, nodule growth rate, specific nodule activity, specific leaf area, and specific internode length. The temperature response equations (Fig 7.1) for these processes and cardinal temperatures are defined in the species file. Similar functions are also used to describe temperature sensitivity of reproductive processes, rate of pod addition, limits on partitioning to reproductive parts, and rate of single seed growth.

At higher than optimum temperature, peanut exhibits poor fruit formation, extended vegetative growth, and poor partitioning and these effects are represented in the model. To account for specific causes like production of vegetative primordia and the expression of more vegetative sites, high temperature induced delay in onset of reproductive sites, and failure of

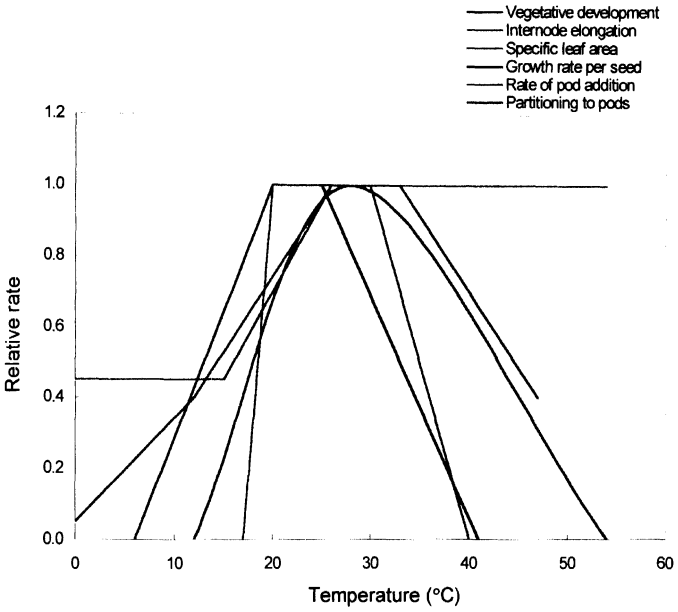


Fig. 7.1 Temperature response functions for relative rate of vegetative and reproductive processes described in PNUTGRO species file. (Source: Boote *et al.*, 1999).

successful fertilisation of reproductive sites, a 'partitioning limit' function has been included. When temperatures >33 °C occur during the pod growth period, there is a decrease in the maximum fraction partitioned to pods.

7.2.3 Multilocation experiments

Three field experiments (in 1993, 1994 and 1995) were conducted at five locations in the SAT of India (Table 7.1 and Fig. 7.2), under an ACIAR-ICAR-ICRISAT collaborative project to identify genotypes for water stress tolerance. These are the main locations where groundnut is cultivated extensively in India. Three irrigation treatments were imposed in each of the locations; irrigated (IRRI), rainfed (RF) and rain-out shelter (ROS), to evaluate the genotypes for water stress tolerance. Data from irrigated and rainfed treatments, was used in this study after obtaining permission from project coordinators (Wright and Nageswara Rao, 1994). The variability in climate (Table 7.1) and soil (Table 7.2 and Table 7.3) is the main reason for choosing locations.

7.2.4 Experimental site details

7.2.4.1 Weather data

Daily weather data, maximum and minimum temperature, solar radiation, rainfall and evaporation were obtained from a weather station located within a distance of 0.5 - 1.5 km from experimental site. In locations where there was no facility to record solar radiation, sunshine hours were used to obtain the solar radiation values. The weather for these locations is presented in Table 7.1.

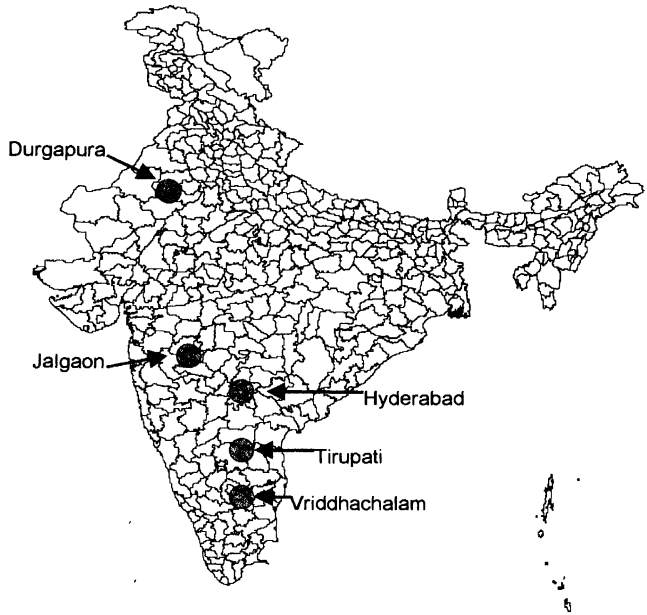


Fig. 7.2 Map of India showing the locations at which drought screening trials were conducted between 1993-1995 under ACIAR-ICAR-ICRISAT collaborative project. (Map not to scale).

7.2.4.2 Soil data

The physical and chemical properties of the top 30 cm of the soils are presented in Table 7.2 and 7.3, respectively. Soil profile data for all the locations were obtained from *Soil Series of India* (1984) published by National Bureau of Soil Survey and Land Use Planning (NBSS&LUP), Nagpur, India. Soils varied from sandy loams to vertisols, with water holding capacities of between 72 and 276 mm. The available total rooting depth was between 100 and 150 cm. Soils also varied in their organic matter and nutrient status (Table 7.3).

7.2.4.3 Rainfall and Irrigation

The amount of rainfall received in each of 1993, 1994 and 1995 during the crop growth period is provided in Table (7.1). The rainfall of these locations, which ranged from 232 to 704 mm, is typical of the SAT. Irrigation was provided by a drip irrigation system and the amount of water supplied to the crop was recorded (Table 7.4). Plants were irrigated at 7 d intervals. The amount of irrigation at each interval was calculated as 0.8 x total evaporation during the 7 d period, where 0.8 is the crop coefficient (Kc) for ET from field during groundnut reproductive period (Doorenbos and Pruitt, 1992).

Table 7.1 Details of latitude, longitude and seasonal weather for the five Indian locations used in the study.

Location	Latitude (N)	Longitude (E)	Date of sowing (Day of year)	Average daily temperature (°C)		Average daily solar radiation (MJ m^{-2})	Total rainfall (mm)	Average daily evaporation (mm)
				Maximum	Minimum			
Hyderabad (HYD)								
1993	17°23'	78°28'	168	30.6	17.5	22.3	660	5.6
1994			171	29.7	15.8	20.7	595	4.6
1995			181	30.1	16.0	22.4	996	4.8
Tirupati (TPT)								
1993	13°39'	79°25'	204	31.9	15.9	23.2	821	4.7
1994			187	32.5	14.2	23.7	680	4.9
1995			188	33.1	14.7	24.5	806	4.8
Vriddhachalam (VRC)								
1994	11°30'	79°20'	199	29.9	15.2	25.8	695	3.6
1995			174	38.3	17.2	25.8	497	3.6
Durgapura (DRG)								
1993	24°38'	76°08'	206	33.3	15.2	20.7	232	5.8
1994			199	30.5	15.5	25.0	452	6.1
1995				32.5	13.8	20.9	598	6.2
Jalgaon (JAL)								
1993	21°00'	75°34'	189	32.0	14.9	20.1	570	4.5
1994			187	31.6	14.2	21.8	734	4.3
1995			181	34.8	14.2	21.6	469	4.4

Table 7.2 Physical properties and moisture characteristics of the top 30 cm of soil for five Indian locations used in the study.

Location	Soil Taxonomy	Physical properties				Soil moisture characteristics				
		Coarse Sand (%)	Fine sand (%)	Silt (%)	Clay (%)	FC (%)	PWP (%)	AW (%)	RD (cm)	TSW (mm)
HYD	Lithic Rhodustalf	2	50	13	34	20	8	12	120	276
TPT	NA	50	31	9	7	10	4	6	120	72
VRC	Udic Rhodustalf	64	22	8	6	18	8	10	100	100
DRG	NA	8	82	6	4	10	4	6	150	90
JAL	NA	12	40	19	29	36	13	23	120	72

(Source: Wright and Nageswara Rao, 1996)

Table 7.3 Chemical properties of the top 30 cm of soil for five Indian locations used in the study.

Location	pH (1:2.5)	EC (mmh)	Organic matter (%)	N (%)	P	K	ExCa	ExMg	ExNa	S
					(mg kg^{-1})					
HYD	8.6	0.06	0.18	0.01	120	70	735	258	74	8
TPT	7.8	0.07	0.72	0.02	60	74	1680	390	145	10
VRC	8.2	0.24	0.81	0.02	100	180	6510	1235	320	10
DRG	8.5	0.15	1.80	0.02	90	160	10830	655	330	6
JAL	5.6	0.04	0.16	0.01	20	35	250	60	75	6

(Source: Wright and Nageswara Rao, 1996)

Table 7.4 Amount of irrigation supplied (mm) and rainfall (mm) received in the five Indian locations used in the study.

Location	Irrigation	Rainfall	Number of rainy days ($> 2.5mm\ d^{-1}$)
	----------mm----------		
HYD			
1993	182	539	47
1994	215	428	41
1995	159	704	52
TPT			
1993	200	567	39
1994	351	338	38
1995	250	594	39
VRC			
1994	230	458	23
1995	220	495	22
DRG			
1993	477	232	12
1994	439	497	28
JAL			
1993	264	547	40
1994	354	530	34
1995	458	338	30

7.2.4.4 Genotypes

Fifty genotypes were evaluated for water stress tolerance in the ACIAR-ICAR-ICRISAT collaborative project. Cultivar ICG 476 (Chico) was selected to calibrate the model for these five locations. This genotype is traditionally cultivated at all the locations and the genetic coefficients for this genotype are available in the PNUTGRO model. The model has also been well calibrated for this genotype. However, there still exits the question of site-specific genetic coefficients due to lack of built-in ability to account for G x E interaction in PNUTGRO. Hence, site specific calibration was also carried out (see section 7.2.6).

7.2.5 Measurements

7.2.5.1 Crop phenology

Dates of sowing, flowering (R1) and physiological maturity (R7) were available from the data sets (Table 7.5). Other stages of reproductive development were obtained from available literature on cultivar ICG 476.

7.2.5.2 Growth analysis

Frequency of plant sampling and sample size was similar at all locations. Harvests were made in all the three replicate plots. Plants were sampled from an area of 0.6 m^2 at 40 and 75 DAS, and at harvest maturity. At each harvest, the plant sample was divided into leaves, stem and pod, which were oven dried at 60 °C for 3-4 d to obtain dry weights. Leaf area and specific leaf area (SLA) were

Table 7.5 Sowing date, time to flowering and harvest maturity during 1993-1995 at five Indian locations used in the study.

Location and Year	Sowing date (Day of year)	Time (DAS) to Flowering	Time (DAS) to Harvest maturity
HYD			
1993 IR	168	28	118
RF		28	103
1994 IR	171	29	116
RF		29	103
1995 IR	181	29	110
RF		29	108
TPT			
1993 IR	204	26	98
RF		26	91
1994 IR	187	28	102
RF		28	96
1995 IR	188	25	110
RF		25	102
VRC			
1994 IR	199	24	101
RF		24	99
1995 IR	174	24	103
RF		24	94
DRG			
1993 IR	206	30	108
RF		30	98
1994 IR	199	26	106
RF		26	99
JAL			
1993 IR	189	25	120
RF		25	108
1994 IR	187	29	111
RF		29	106
1995 IR	181	27	101
RF		27	99

also calculated from each sample. Final pod yield and biomass were calculated from a harvested area of more than 2.0 m^2, the precise area varied with location (Wright and Nageswara Rao, 1996).

7.2.6 Model data entry

The database management system of the Decision Support System for Agrotechnology Transfer (DSSAT v3) was used to enter crop, weather, irrigation and soil data into computer.

7.2.7 Model calibration

The model was calibrated for each of the locations following the systematic approach as described by Boote (1999). The calibration of the PNUTGRO to different locations is described in the steps below.

STEP 1 Crop life cycle (flowering and harvest maturity)

The crop development was adjusted using the actual weather data. The two main factors that were calibrated for setting the right flowering and maturity date are EM-FL (photothermal days between plant emergence and flower appearance) and SD-PM (photothermal days between first seed and physiological maturity).

STEP 2 Dry matter accumulation

The main factor in the model, which determines the slope of dry matter accumulation, is SLPF (soil fertility function in the soils file). This assumes that the site differences in fertility create the differences in biomass. This factor,

inadvertently, also accounts for diseases and pests effects on crop growth and yield. Incidence of spodoptera and thrips was recorded in experimental plots at all the locations but with varying intensity. Control measures were taken to contain the pest damage to avoid economic threshold damage. For irrigated experiment of each year at each location SLPF was determined so that the predicted final biomass was as close as possible to the observed biomass at harvest maturity. Then, SLPF was averaged over three years for the genotype to give location SLPF, and the value so obtained was used to simulate the biomass and pod yield.

The slope of predicted dry matter accumulation was made similar to that of the observed by adjusting both SLA and LAI. The factor SLAVR was used to adjust SLA, and LAI was adjusted using the factor FL-LF (time from flowering to maximum leaf area).

STEP 3 Pod yield

The timing from flowering to first pod (FL-SH), the timing from first flower to first seed (FL-SD) and duration of pod addition (PODUR) were adjusted to get the initial rise in pod dry weight and seed dry weight. Maximum fraction of daily growth that is partitioned to seed + shell is determined by this factor XFRT. This determines the partitioning of dry matter between leaf, stem and pod. This factor also takes into account the indeterminate habit of peanut plants, where vegetative growth occurs even during the pod filling periods. For each experiment, at a given location for a genotype in a year, XFRT was determined.

The XFRT was calculated for each year for the genotype at each location and the location average (over three years) value was used to simulate the pod yield.

7.2.8 Water stress x high temperature simulations

7.2.8.1 Experimental data

The crop, soil, weather, and irrigation data from the field experiment, (Chapter 6) were used in this study. Groundnut cultivars, TMV 2 and ICGS 11, from field study were used for the simulations.

7.2.8.2 Model data entry

The database management system of the Decision Support System for Agrotechnology Transfer (DSSAT v3) was used to enter crop, weather, irrigation and soil data into computer.

7.2.8.3 Model Calibration

Calibration of the model is essential in order to validate the model response to high temperature. The calibration was essential as the crop was grown during the summer of 1999 at ICRISAT in India, the period in which the crop is not normally cultivated. The control treatment in Chapter 6, T1D1, was used to calibrate the model.

The calibration of crop life cycle, biomass and pod yield for each of the cultivars, TMV 2 and ICGS 11, in this study was carried out separately as described in

steps 1-3 of section 7.2.7. The cultivar specific coefficients, given in PNGRO980.CUL file, are used to define the development of cultivar under the given weather and management. TMV 2 is a widely grown cultivar in India and this genotype has been evaluated using PNUTGRO. Hence, the genetic coefficients for this genotype are available in the model and were adapted to the specific management conditions under study. There are no genetic coefficients available for ICGS 11 in the model. Hence, the coefficients of ICGS 11 were estimated by the procedure described by Boote *et al.* (1989) and Singh *et al.* (1994a). The 11 phenological coefficients for each of these cultivars were determined so that the growth and development of control treatment were close to those of the simulated values (Table 7.6). The values that gave the most realistic and closer predictions to results in Chapter 6 were used in this study.

7.2.9 Data comparison (Observed vs Predicted)

In many modelling studies, a scattered diagram is used to compare observed and predicted values. A linear regression is then used to fit a straight line between observed and predicted values (Smith and Rose, 1995). Fitted linear regression requires testing with parametric or non-parametric statistical tests to determine whether the intercept is equal to zero and the slope is equal to or not significantly different from unity. However, Harrison (1990) and Mitchell (1997) argued against using linear regression as a validation tool because of its inappropriateness and violation of assumptions associated with using regression as a tool, and difficulties experienced in accrediting a null hypothesis. Mitchell (1997), and Mitchell and Sheehy (1997) provided an alternate objective and

simple method, free of *a priori* assumptions. This method uses deviation (observed minus predicted) plotted against the observed values and specifies two criteria for adequacy of the model. They are the envelope of acceptable precision and proportion of points that must lie within the envelope. In this method, no statistical tests are involved and hence the problem of satisfying assumptions is avoided. Therefore, the deviation method of Mitchell and Sheehy (1997) was used in this study to compare the predicted values with observed. The envelope of acceptable precision used in this study is ± SD (standard deviation) of observed values.

7.3 RESULTS

7.3.1 Multilocation weather

The crop was not exposed to water stress, at any of the locations, in the irrigated treatment. Under rainfed conditions, the crop was subjected to long periods of dry spells at Vriddhachalam (VRC) and Durgapura (DRG) and to moderate dry spells at other locations (Table 7.4).

Temperatures to which different crop growth stages were exposed are presented in Table 7.6. Except at Hyderabad, the crop in the other locations was exposed to high temperatures (>34°C) during both the observed vegetative (S-FF) and reproductive phases (FF-PM). Occurrence of high temperatures was more frequent during the reproductive phase of the crop growth. Number of days with high temperature during the reproductive phase ranged from 10 to 84 d. Year 1995 was particularly hot in all the locations expect at Hyderabad.

7.3.2 Model calibration for five locations

7.3.2.1 Time to flowering and physiological maturity

Time to flowering and harvest maturity was calibrated only for one year at a location using the weather data and that resulted in reliable prediction in other years at a given location. The SD value indicating the acceptable limit for time from sowing to flowering was 2.07 d. The model predicted the time to flowering and harvest maturity within acceptable limits (Fig 7.3). Time from sowing to flowering in ICG 476 in the five locations ranged from 24 to 30 d. However, there was a systematic deviation of the predictions that can be attributed to constant

prediction by the model for flowering and physiological maturity in multiple environments used in the study.

Table. 7.6 Average temperature (day/night) recorded during different stages of crop development and number of days with maximum temperatures exceeding > 34°C during the crop period at five multilocation experimental sites. (S = sowing; FF = first flower; FS = first seed; PM = physiological maturity).

Location	Temperature °C (day/night)				Days with temperature >34°C (d)	
	S-FF	FF-FS	FS-PM	S-PM	S-PM	FF-PM
HYD						
1993	33/23	31/22	29/22	30/22	11	0
1994	29/22	30/23	30/21	30/22	0	0
1995	29/22	30/23	30/22	30/22	2	0
TPT						
1993	35/25	34/25	32/23	33/24	30	18
1994	34/26	33/24	33/24	33/24	42	31
1995	33/25	34/25	33/24	33/24	35	23
VRC						
1993	34/26	34/26	31/26	32/26	24	10
1994	30/25	30/26	30/26	30/26	0	0
1995	38/25	39/26	38/26	38/26	107	83
DRG						
1993	33/25	36/24	34/21	34/22	64	48
1994	31/24	31/24	33/20	32/22	26	20
JAL						
1993	31/23	31/23	32/22	32/23	24	13
1994	30/23	30/23	32/21	32/22	33	30
1995	33/24	32/23	34/23	34/23	66	56

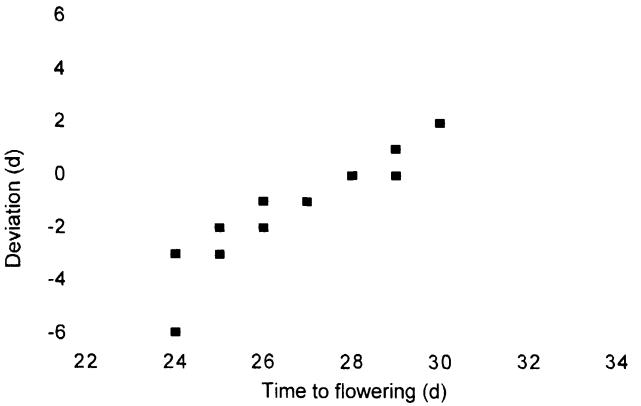


Fig. 7.3 Deviations of observed values from predicted days from sowing to flowering grown under irrigated (IR - ■) and rainfed (RF - □) conditions at five locations in India during 1993 to 1995.

Observed time to flowering was similar under irrigated or rainfed conditions. Predicted time to flowering also did not vary with irrigated and rainfed treatments. Around 80% of the predicted values were in the acceptable range. The predictions for time to flowering deviated less in the observed values range of 26-29 DAS, an increase or decrease in this range of observed flowering deviated the predicted values from the acceptable envelope of SD. There was more variation in prediction of time to physiological maturity compared to flowering (Fig. 7.4). The SD for observed values was 7.02 d and was used as the acceptable envelope. The model delayed the time to physiological maturity when compared to the observed values. The delay was greater under rainfed conditions than when compared to irrigated crop. Of the predicted values 38% were outside the acceptable range.

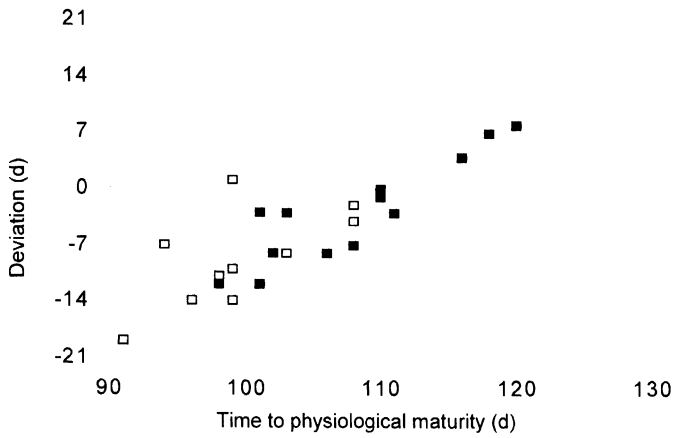


Fig. 7.4 Deviations of observed values from predicted days from sowing to physiological maturity under irrigated (IR - ■) and rainfed (RF - □) conditions grown at five locations in India during 1993 to 1995.

7.3.2.2 Soil fertility factor (SLPF)

Once the crop cycle was adjusted in the model, changes in the SLPF factor were necessary to bring the predicted values of biomass closer to the observed. No changes in LAI and SLA (genetic coefficients of ICG 476) were required to predict the biomass. Soil fertility factors used for calibrating the model to predict the observed biomass and pod yields are presented in Table 7.7. The SLPF values varied from year to year at a given location and between locations indicating the site to site variability in the study. The values ranged from 0.58 (Hyderabad) to 1.19 (Jalgaon). Using the yearly SLPF and location SLPF (average of three years), both biomass (Fig. 7.5a) and pod yield (Fig. 7.5b) were predicted.

Table 7.7 Yearly and location average SLPF values obtained by calibrating the model for five locations used in the study.

Location	Soil fertility factor (SLPF)
HYD	
1993	0.65
1994	0.58
1995	0.78
Average	0.67
TPT	
1993	0.85
1994	0.82
1995	0.68
Average	0.78
VRC	
1994	0.80
1995	0.55
Average	0.68
DRG	
1993	0.86
1994	0.78
Average	0.82
JAL	
1993	0.93
1994	1.13
1995	1.19
Average	1.08

Results indicate that the deviations were randomly scattered above and below the reference zero line. Deviation results either with yearly SLPF or with location SLPF were similar. The average SD value of 2528 kg ha^{-1} and 1089 kg ha^{-1} for observed biomass and pod yield, respectively, was used as the acceptable envelope. More than 95% of the points lie within the acceptable envelope. This indicates that a location average SLPF can be used in PNUTGRO to predict the crop growth, avoiding yearly calibration of the model.

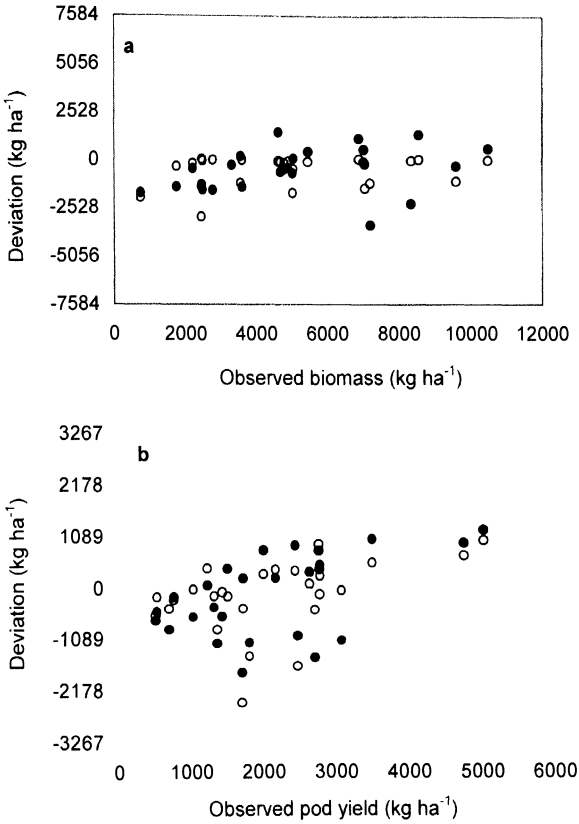


Fig. 7.5 Deviations of observed values from predicted biomass (a) and pod yield (b) using yearly SFPL (○) and location SLPF (●), irrespective of the irrigation treatment, at five locations in India during 1993 to 1995.

7.3.2.3 XFRT

There was no need to change the built-in XFRT factor in the model. A value of 0.8 estimated pod yields and crop biomass to an acceptable extent as described in section 7.3.3.

7.3.3 Simulation of biomass, pod yield and HI in IR and RF at five locations

The deviations of observed from predicted values of biomass, pod yield and HI are presented in Fig. 7.6, Fig. 7.7 and Fig. 7.8, respectively. The deviations of pod yield against the number of days with high temperature at various locations are presented in Fig 7.9. The percentage of points with the acceptable envelope (±SD) varied with the component predicted. Results show that the deviations for pod yield and biomass were randomly scattered above and below the reference zero line and more than 90% of points lie within the envelope indicating the performance of the PNUTGRO model. The predicted values of biomass and pod yield under rainfed conditions lie more closely to the zero line, indicating greater confidence of model predictions under rainfed conditions.

Predicted values for irrigated treatments are scattered all over the envelope. Biomass was predicted with more confidence than the pod yields. Predictions made using SLPF of each year or average SLPF for three years over a given location did not alter the deviations of the predicted from the observed. The model was less efficient in predicting the HI for the various locations for which the simulations were carried out. More than 35% of the deviations lie beyond the acceptable envelope.

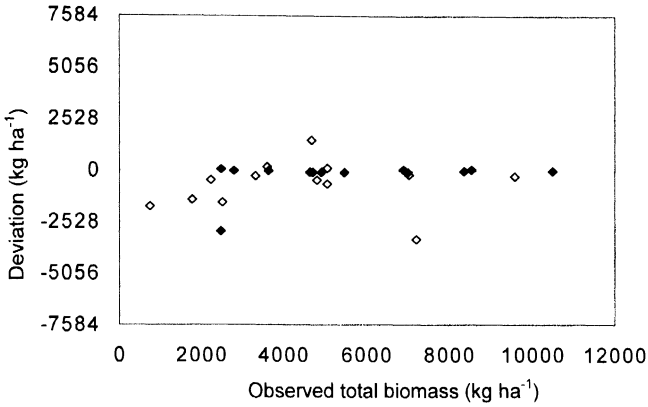


Fig. 7.6 Deviation of total observed values from predicted biomass durir 1993-1995 in irrigated (♦) and rainfed (◊) treatments from five locations India. The envelope of acceptable precision is ±SD.

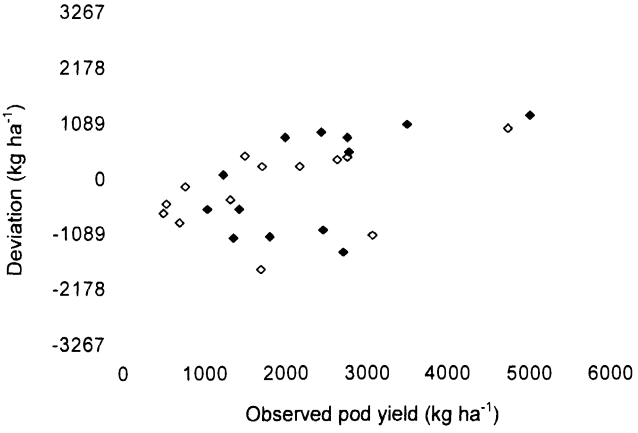


Fig. 7.7 Deviation of total observed values from predicted pod yield during 1993-1995 in irrigated (♦) and rainfed (◊) treatments from five locations in India. The envelope of acceptable precision is ±SD.

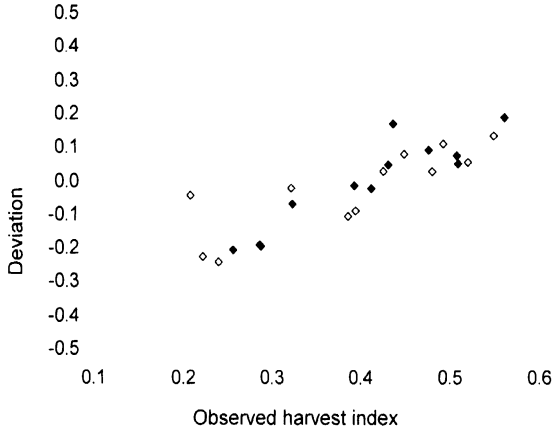


Fig. 7.8 Deviation of observed values from predicted harvest index during 1993-1995 in irrigated (♦) and rainfed (◊) treatments from five locations in India. The envelope of acceptable precision is ±SD.

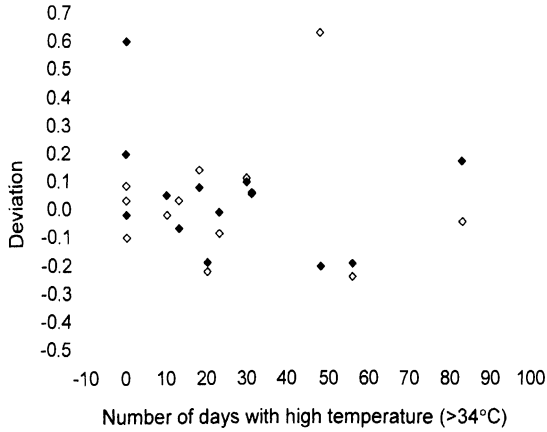


Fig. 7.9 Effect of number of days with high temperature on deviation of observed from predicted harvest index during 1993-1995 in irrigated (♦) and rainfed (◊) treatments from five locations in India. The envelope of acceptable precision is ±SD.

The number of days with high temperature could not account for the deviation in the predicted pod yields from observed. No particular pattern of distribution deviation, either increasing or decreasing could be observed in these locations.

7.3.4 Water stress x high temperature

Simulations were also carried out for the field experiment done in summer of 1999 in Red loamy soils of ICRISAT, Hyderabad, India, described in Chapter 6. In this simulation study, the ability of PNUTGRO to account for the effects of high temperature and its interaction with water stress were tested. The T1D1 treatment (control) was used to calibrate the model for each of the genotypes, TMV 2 and ICGS 11, used in the study. The deviations of the observed values from predicted are presented in Fig. 7.10 and 7.11.

The predictions indicate that the model was capable of predicting the pod yields and harvest index with a greater precision than the biomass. Biomass prediction for high temperature treatments T2D1, T2D2 and T4D2 in both the genotypes was lower compared to the observed values (Fig. 7.10a). The predicted values for biomass in other treatments were within the acceptable envelope. For pod yield (Fig. 7.10b) and harvest index (Fig. 7.11a) predictions, less than 20% of the deviations were outside the acceptable envelope and the spread of the observations was greater.

Increase in temperature (T1 to T4) or combination of temperature with water stress treatment resulted in the deviations of observed from predicted to be

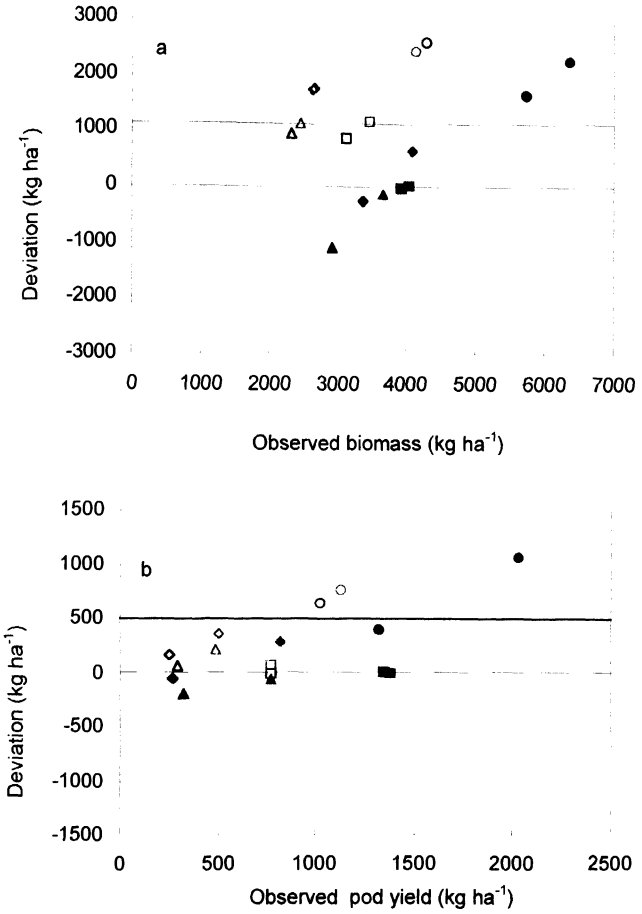


Fig. 7.10 Deviation of total observed from total predicted biomass (kg ha^{-1}) (a) and pod yield (kg ha^{-1}) (b) during summer of 1999 at ICRISAT, Hyderabad, India (Chapter 6). The envelope of acceptable precision is the standard deviation (S.D.). (Black - TMV 2, Red - ICGS 11, closed - 100% ASM (D1), open - 40% ASM (D2), square - T1, circle - T2, triangle - T3, diamond - T4).

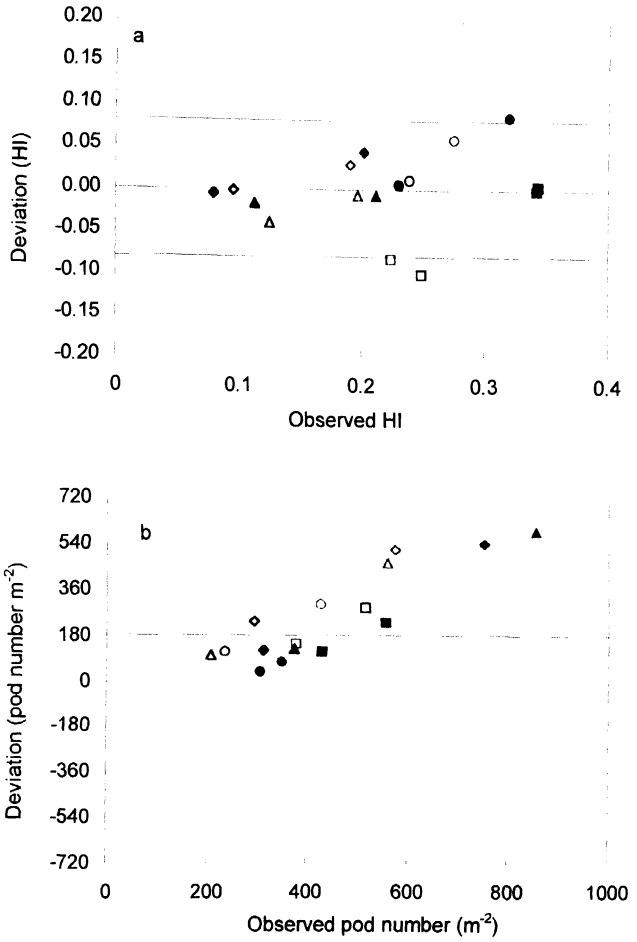


Fig. 7.11 Deviation of total observed from total predicted harvest index (HI) (a) and pod number (m^{-2}) (b) during summer of 1999 at ICRISAT, Hyderabad, India (Chapter 6). The envelope of acceptable precision is the standard deviation (S.D.). (Black - TMV 2, Red - ICGS 11, closed - 100% ASM (D1), open - 40% ASM (D2), square - T1, circle - T2, triangle - T3, diamond - T4).

randomly distributed and moved the deviations farther away from the zero line. These deviations were much greater for biomass under water stress than irrigated treatments. Observed pod number (m^{-2}) deviated significantly from the predicted number. Figure 7.10b shows that 50% of the deviations of pod number lie outside of the acceptable envelope. The model under-predicted the pod number in all the treatments. Of the outliers, 65% are from water stressed treatments. The model predicted the values for TMV 2 with greater confidence than for ICGS 11. The deviations recorded were greater in the high temperature treatments T3 and T4 of ICGS 11 maintained at 100% ASM. Although the deviation was less when T3 and T4 were subjected to 40% ASM, but remained outside the acceptable envelope.

7.4 DISCUSSION

The simulation predictions of multilocation experimental data indicated that the factor SLPF can be used to calibrate PNUTGRO in order to give a reliable estimate of groundnut yields in a given location. Crop yields for a given location can be predicted by altering the single factor SLPF, if soil characters of the area are known and the weather predictions made are a reliable estimate corresponding to the base climate for the location. Such simple, location specific, factors are essential if reliable yield forecasts and predictions are to be made for large cultivated areas (district or state) such as those in India.

The SLPF factor accounts for the variation in the soil fertility from site to site and for the biotic stress factors (insect and disease damage) (Boote *et al.*, 1998;

Singh *et al.*, 1994a). The model has a well-built subroutine for predicting the nitrogen use by the crop supplied in either inorganic or organic form or through symbiotic nitrogen fixation (Boote *et al.*, 1998). Hence, the model can only account for the location to location variation in the soil nitrogen availability and supply. The model does not account for the use of other major nutrients like P and K and the role of other essential nutrients for groundnut growth and development. The inability of the model to account for pest and disease damage further weakens the model capability to predict biomass and pod yield. The use of this SLPF factor weakens the dynamic simulation capability of the model when coupled with weather prediction models to predict groundnut yields (Hansen and Jones, 2000). Hence, improvement of the soil routines of PNUTGRO and incorporation pest routines is essential if the use of SLPF is to be avoided to couple the model with weather prediction models.

Climate change is inevitable (IPCC, 2000) resulting in a severity of water stress and extremes of high temperature in the SAT. Crop models can act as surrogates to estimate the crop yield shifts in future climates predicted by the climate models. The multilocation simulation study and the simulation of the results from Chapter 6, discussed below, indicate that PNUTGRO needs to be modified for yield predictions under future climates.

Of the irrigated and rainfed treatments simulated by the model, greater precision in prediction is attached to those under rainfed conditions. The greater precision under rainfed conditions is required for yield predictions as > 80% of groundnut

crop area in India is under rainfed cultivation (Agricultural Situation in India). Such greater precision for prediction of biomass and pod yield under rainfed conditions compared to irrigated treatments was also observed by Singh *et al.* (1994a) in the SAT of India. The reasons for this were attributed to the greater pest and disease damage, which the model cannot account for, in the irrigated treatment compared to rainfed treatment. Similar observations for higher incidence of pest and disease were also made at different locations in irrigated treatments.

Simulations of the effects of water stress x high temperature indicated that the predicted values were mostly lower than the observed values. The deviations were greatest in the high temperature treatments. The predictions were close to the zero line for TMV 2, a moderately heat tolerant cultivar, but the observed values of ICGS 11, also a heat tolerant cultivar, were much higher than the predicted values. This difference between genotypes was due to higher biomass and pod yield observed in ICGS 11 than in TMV 2 under field conditions (Chapter 6). The results from the field study show that under high temperature conditions a tolerant cultivar produces large biomass and in turn results in higher pod yield without a significant change in the harvest index.

The model was unable to account for the excessive vegetative growth under high temperature conditions and failed to identify the genotypic differences in temperature response. The main reason for this is that there are no crop-specific subroutines for temperature response in the model. The PNUTGRO uses the

source code of CROPGRO, which is for a family of legumes - soyabean, groundnut, dry bean and chick pea. There is a common FORTRAN code, all species attributes are input from species files, as well as ecotype and cultivar files. Many of the subroutines such as photosynthesis, partitioning have been derived from soyabean and modified to suit groundnut (Boote *et al.*, 1986).

In the words of model developers (Boote *et al.*, 1999): "We have less information on differential phase sensitivity to temperature in the groundnut and dry bean model, but we believe that the basic concept is correct and the approach gives the needed flexibility". The results presented in the thesis (Chapters 3, 4, 5 and 6) and by Craufurd *et al.* (2000); Vara Prasad *et al.* (1998, 1999b, 2000a) indicate that groundnut behaves differently from other legumes in terms of having greater optimum and ceiling temperatures for various growth and reproductive processes. These results also show significant genotypic differences for temperature response. Hence, temperature response functions in PNUTGRO need to be modified for physiological and growth processes in groundnut to simulate the experimental results.

Another reason for greater deviations in biomass and pod yield of ICGS 11 when compared to TMV 2 under high temperature can be attributed to the carbon-based nature of PNUTGRO model (Boote *et al.*, 1998, 1999). As vegetative growth is under-predicted by the model under high temperature, a decrease in vegetative growth reduces the amount of assimilates available for the addition of new classes or cohorts of pods that are added on a daily basis (Boote *et al.*,

1986). Thus, addition of pods is stopped in the model under high temperature conditions. Under field conditions, the addition of flowers and pegs, and in turn pods, is reduced only moderately in TMV 2 and not stopped in the tolerant cultivar ICGS 11. However, the partitioning of assimilates required for pod development is severely reduced in TMV 2 and not in ICGS 11. Deviations for pod number are much greater in ICGS 11 than in TMV 2 as the pod number produced under field conditions by ICGS 11 is significantly greater than TMV 2 (Chapter 6). Therefore, the partitioning function in the PNUTGRO should be modified to account for these temperature and genotype effects.

The model detects that at higher than optimum temperature, peanut exhibits poor fruit formation and poor partitioning (Boote *et al.*, 1998). However, the model failed to account for the pod number difference between the tolerant and susceptible genotype. This is because flower production and the rate of pod production in PNUTGRO is a set number, which is not genotype specific. It can be observed from Chapters 3 and 6, and from Craufurd *et al.* (2000) that flowering pattern and rate are genotype specific within a given ecotype. Incorporating certain genotype specific coefficients that can identify the rate and pattern of flowering of a given genotype would make the model more sensitive to high temperature environments.

7.5 CONCLUSIONS

The simulation study shows that SLPF (soil fertility factor) can be used as a location specific variable for forecasting or predicting the yield of irrigated and

rainfed groundnut in the SAT. The study suggests that there is a need to modify the temperature response functions in PNUTGRO to make them reliable predictor of groundnut growth and development in the SAT. Genotype specific coefficients for flowering are necessary in the model to clearly identify the genotype differences in pod yield for a given environment. The modifications for temperature response are essential to predict groundnut yields under current and predicted hot climates.

CHAPTER 8

GENERAL DISCUSSION

Crop productivity in the SAT is often limited by water stress (WS) and high temperature (HT). The occurrence of these two stresses is widespread in areas where groundnut is cultivated (Ong, 1984; Greenberg *et al.*, 1992). Flowering and pod development stages are critical in groundnut growth and development susceptible to water (Williams *et al.*, 1986; Stirling *et al.* 1991; Reddy and Reddy, 1993) and high temperature stress (Vara Prasad *et al.* 1998, 1999a, 1999b, 2000). The spread of groundnut cultivation to non-traditional areas in Rajasthan and Gujarat states in India (Fig. 8.1a), due to increase in area under irrigation (Fig. 8.1b), is increasing the risk of exposure to environmental extremes.

The current environmental extremes are likely to increase in severity under the predicted climatic change scenarios (IPCC, 2000). In its assessment of climate change, IPCC (2000) stated that " although it is not clear which regions are to be most affected by climate change, the ones that most suffer will lie near or in the tropics". Mitchell and Hulme, (2000) in their study on climate predictions indicate a 6°C increase in current mean temperature during this century of countries like India. Hence, it is necessary to sustain and increase productivity of nutrition rich crops like groundnut to feed the ever-growing population in these vulnerable regions. For example, the population of India crossed a billion in May 2000. Groundnuts are also a very valuable fodder both, as hay and cake, and animals will benefit from sustained productivity.

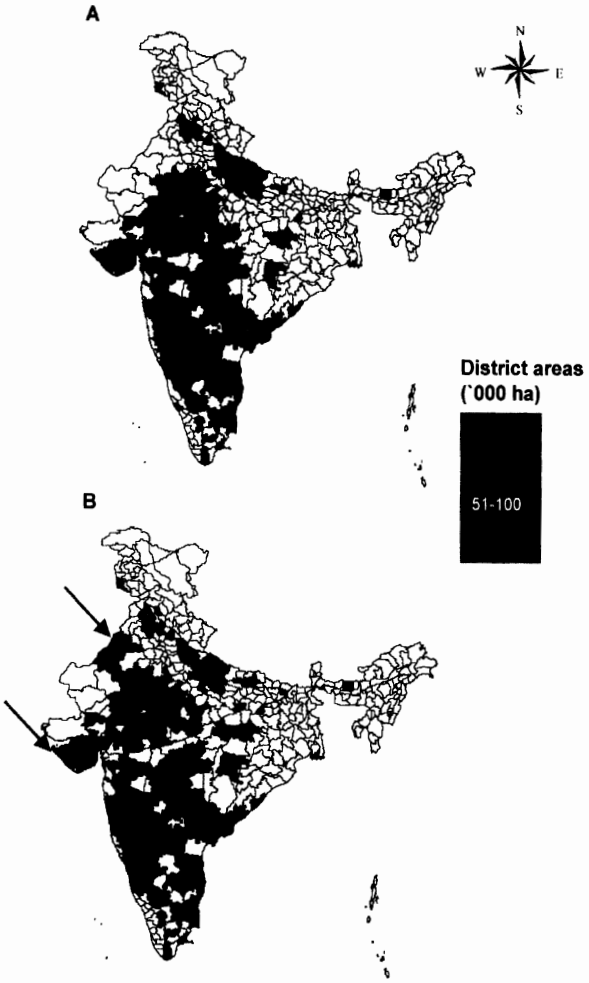


Fig. 8.1 Districts with groundnut cultivation in 1966 (A) and in 1990 (B). Arrows point spread of groundnut cultivation to areas with extreme climates (Source: Agricultural Situation in India). Not to scale.

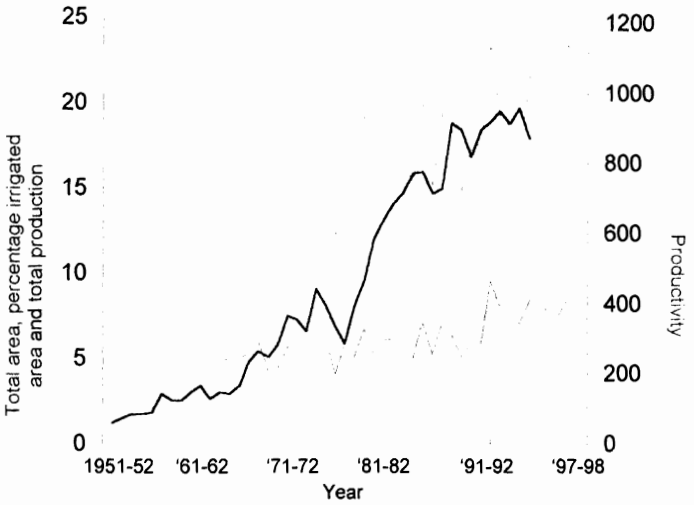


Fig. 8.2 Yearly area (- m ha), production (- m ton's), productivity (- kg ha^{-1}) and percentage area under irrigation (-) of groundnut in India from 1951 to 1998. (Source: http://www.nic.in/agricoop/statistics/ground.htm).

Studies conducted so far to improve productivity of groundnuts have concentrated on the individual effects of water stress (Nageswara Rao *et al.*, 1988; Stirling *et al.*, 1991; Wright *et al.*, 1991; Chapman *et al.*, 1993a) or temperature stress (Ketring, 1984; Ong, 1986; Craufurd *et al.*, 1999; Wheeler *et al.*, 1997; Vara Prasad *et al.*, 1998), even though both stresses occur together in groundnut growing regions. Therefore, it is necessary to identify the role of each of these stresses, separate and combined, in reducing yields in SAT, and identify their effects on growth, development and the physiological processes responsible for yield reductions.

Duncan *et al.* (1978) gave the simple yield model (equation 8.1) to describe the yield of groundnut,

$$Y_{pod} = pCD_r \qquad [8.1]$$

where, Y_{pod} is pod yield, p is partitioning or harvest index (HI), C is crop growth rate and D_r is reproductive duration. The components of this equation are controlled by various physiological processes, identified in this study, as shown in the Fig. 8.3. The main factors that determine the yield of a crop are its genotype and the environment. In this study, we see how the genotype and the main environmental factors - temperature and water stress, control groundnut yield. We also discuss the measures required to sustain yield in SAT.

Water stress x high temperature interaction studies were carried out under both controlled environment (Chapter 3) and field conditions (Chapter 6). Water stress under both controlled environment and field conditions reduced the vegetative

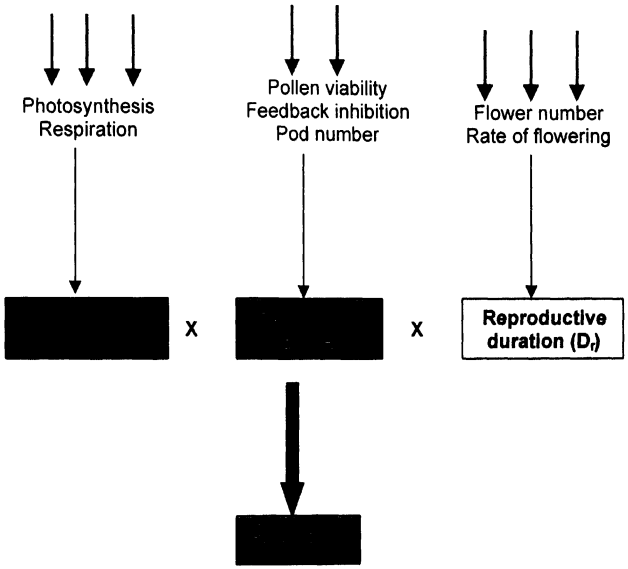


Fig. 8.3 Effect of temperature (▼), water stress (▼) and genotype (▼) on the physiological processes identified in this study and their influence on the components of Duncan *et al.* (1978) pod yield model.

growth due to a reduction in crop growth rate (C). High temperature (37°C) in the controlled environment had no effect on vegetative growth, while under field conditions temperatures greater than >40°C slightly reduced the vegetative growth and C. The results from these experiments reveal that there exists an interaction between water stress and high temperature which is negative for vegetative components (C). The severity of the interaction effects depends on the stage of crop and the severity of stress. No interaction was found for pod yields in these studies (Chapters 3 and 6), although both the stresses reduced pod yield. These studies conclude that different mechanisms operate in inducing tolerance to water and high temperature stress.

Yield reduction due to water stress (Chapter 3 and Chapter 6) is a result of reduced assimilate accumulation (C) and decrease in flower number. The reproductive duration (Dr) modifies final pod yield if successful flower production and fruit-set occurs during this period. Water stress hampered flower production during the Dr, thus reducing the contribution of Dr to final pod yield. Both early water stress and late water stress during the reproductive duration were on par with each other in reducing pod yields. On the other hand, the effects of high temperature are instantaneous resulting in decrease of pod yield. Plants recover after withdrawal of the heat stress and yields of plants grown in optimum temperature or exposed to short periods of high temperatures are similar at maturity. There is no decrease in assimilate accumulation (C) or flower number (D_r) during or immediately after the withdrawal of heat stress, but a decrease in

pod yield occurs. Hence, reduction in pod yield can be attributed to instantaneous failure in fertilisation of groundnut flowers by high temperature. Earlier studies of Vara Prasad *et al.* (1998; 1999; 2000) have identified that pollen production and viability to be inhibited under high temperatures. The role of pollen is discussed later in the chapter.

In controlled environment studies imposition of sudden high temperature treatment follow a square wave pattern (Vara Prasad *et al.*, 1998; 1999; 2000; Wheeler *et al.*, 1997, Craufurd *et al.*, 1999; Chapter 3 and 5). High temperature treatments imposed in controlled environment act on the plant processes from dawn to dusk, i.e. for 12 h period, and bring out the response in the genotype that may not have occurred under field conditions. The reason for this is that temperature follow a sinusoidal pattern under field conditions (Fig. 6.1) and the effect of high temperature extends to a maximum of 3-4 h. A rise in temperature under field conditions by 7-10°C over the ambient can be obtained by covering the plants with clear polythene sheet (Chapter 6). Hence, it is necessary to carry out such high temperature studies under field conditions by using bubbles, but extra care should be taken to control humidity in bubbles.

The results from the field study (Chapter 6) confirm the results from controlled environment experiment (Chapter 3). The interaction between water stress and high temperature is instantaneous on fruit-set and pod number and disappears as high temperature is withdrawn. The slightly greater decrease of pod number under field conditions (46%) compared to controlled environment (46%)

conditions can be attributed to the slightly longer duration (20 d) and higher intensity of temperature (43°C). Even though the intensity and duration of temperature were higher in field, the comparatively lower reduction in yield can be attributed to the greater tolerance of the genotypes TMV 2 and ICGS 11 used in the field study, which was established in the pollen study. Similar decrease in pod number of 50% (Vara Prasad *et al.*, 1998, 2000a) and 33% (Ketring *et al.*, 1984) on exposure to air temperature of 38°/22°C and 35°/22°C (day/night) respectively were recorded in earlier studies.

Increase in temperature during the crop growth period under field conditions reduced the harvest index; i.e. partitioning (p) of assimilates to the developing sink. As can be seen from equation 8.1, any decrease in HI is bound to reduce pod yields. In a recent publication, Ntare *et al.* (2001) established that partitioning (HI) is an important factor governing pod yields under high temperature conditions of Sahelian environments of Africa. Yield improvement under non-stress conditions in groundnut has been achieved through increase in partitioning (HI) (Duncan *et al.*, 1978). This improvement in HI was made possible by manipulating phenology – early flowering, pegging and pod development (Harris, 1988; Mathews *et al.*, 1988; Chapman, 1989) that are components of the reproductive duration (D_r).

The reasons for decrease in HI under high temperature have been established in other crops. Reduction in HI due to high temperature was recorded in cowpea (Nielsen and Hall, 1985; Ismail and Hall, 1998). High temperature accelerated

grain development and reduced the duration of cell division and dry matter accumulation in wheat (Nicolas *et al.*, 1984). Under high temperature conditions conversion of sucrose into starch and reducing sugars is either inhibited or slowed down in the sink. This feedback inhibition from sink reduces the amount of assimilates translocated to the developing grain (wheat – Nicolas *et al.*, 1984; tomato – Dinar and Rudich, 1985). The enzymes involved in starch and sugar metabolism (e.g. AGPase, Sucrose synthase, Soluble starch synthase, Glucokinase) are reduced in their activity by high temperature. In addition to this, a greater demand from the already established sink results in decrease of assimilates translocated to the newly formed sink resulting in their abortion (Dinar and Rudich, 1985). The role of these various processes in groundnut yield reduction due to high temperature is yet to be established.

To bring out the true genotypic differences for heat tolerance, Levitt (1980) suggested that the plants should be exposed to acclimating temperatures prior to imposition of heat stress treatments. To account for this an acclimation study was carried out under controlled environment conditions (Chapter 5). In this study, acclimating temperatures (34°C) for 6 d prior to high temperature (40°C) treatments did not modify the reaction of groundnut genotypes to high temperature. Hence, the genotypic tolerance of 55-437 over ICGV 92116 to high temperature was due to the base heat tolerance. Similar observations to this were made in wheat genotypes by Stone and Nicolas (1995). The acclimation study also revealed that later stages of development i.e. post-anthesis are more tolerant to high temperature than the pre-anthesis i.e. microsporogenesis. This is

supported by the observations made by Slafer and Rawson (1995) that cardinal temperatures for phenological stages rise steadily with plant development. They also suggested that later the phase or development or process in the crop cycle, the higher the base temperature.

The genotypes used in the experiments reported here differed in their relative tolerance to water stress and high temperature. The reasons for differences in yield reduction in groundnut genotypes under water stress are well established, and specific characters have been identified to select genotypes for water stress tolerance, like SLA, HI and biomass (Mathews *et al.*, 1988; Williams *et al.*, 1986; Nageswara Rao *et al.*, 1988; Wright *et al.*, 1991; Nigam *et al.*, 1991). Genotypes in controlled environment interaction study differed in their tolerance to water stress. ICGV 86015 was more tolerant than ICG 796, due to relatively quicker and greater flower production and greater partitioning of biomass to pod yield in ICGV 86015 than in ICG 796, even though ICG 796 had higher biomass. No such genotypic differences in response to high temperature could be recorded in the controlled environment study. The acclimation experiment showed that genotype tolerance to high temperature is due to base tolerance, and that genotypes ICGV 86015 and ICG 796 had similar tolerance to high temperature.

In the field study genotypes differed significantly for pod yield under both water stress and high temperature. Genotype ICGS 11 was tolerant to high temperature compared to TMV 2. The lesser decrease in pod yield of ICGS 11 with increase in temperature during the crop growth was due to its maintenance

of higher HI (*p*) with increase in temperature. Flower number also slightly increased in ICGS 11. In contrast, flower number decreased, fruit-set and pod number, all contributing to Dr, decreased in TMV 2. In TMV 2 a drastic fall in HI (*p*) with increase in high temperature was recorded resulting in significantly lower pod yields. Hence, decrease in pod yield under field conditions is mainly due to a decrease in HI or partitioning (*p*) of biomass to pod yield; the reasons for such a decrease have been explained earlier. These studies thus confirm that the role of reproductive duration (D_r) in inducing tolerance to high temperature and water stress. The genotypes tested in this study are summarised in table 8.1 for their tolerance to high temperature and water stress.

Table 8.1 Summary of the genotype contribution to components of Duncan's equation in inducing tolerance or susceptibility for high temperature and water stress.

Genotype	Components of Duncan's equation			Tolerance to	
	HI	C	Dr	High temperature	Water stress
ICGV 86015	***	**	***	MT	T
ICG 796	**	***	*	MT	S
TMV 2	**	**	**	S	MT
ICGS 11	***	***	***	T	T
55-437	-	**	***	T	T
ICGV 92116	-	***	**	S	S

(- = not studied; *,**,*** indicate relative contribution to the components by the genotype, increase in star number indicates increased contribution; S = susceptible; MT = moderately tolerant; T= tolerant)

High temperature tolerance has been identified in groundnut genotypes in this study and by other researchers (Greenberg *et al.*, 1992; Wheeler *et al.*, 1997; Vara Prasad *et al.*, 1998; 1999; 2000; Craufurd *et al.*, 1999; 2000; Ntare *et al.* 2001). An effective breeding program is required to screen groundnut genotypes for high temperature tolerance. Before a breeding program is designed, Hall (1990) suggested that: (1) the target environment, (2) type of hot weather, (3) stage of growth and processes, and (4) inheritance of high temperature tolerance at critical stage need to be identified. The characters that identify tolerance of the genotype should be easily transferable either by traditional breeding or by molecular biology techniques and strongly associated with high pod yield. Some simple characters, for example SLA for water stress (Nageswara Rao *et al.*, 1988), need to be identified to screen the genotypes for high temperature tolerance.

Tolerance to high temperature exists in several other crops that was associated with specific genes. In cowpea genotypes, Prima and TVu 4552, tolerance to high temperature during pod set is due to a dominant gene (Marfo and Hall, 1992) while recessive genes confer tolerance to high temperature during floral bud and seed coat development (Patel and Hall, 1988; Hall, 1992). This genetic tolerance to high temperature was linked to membrane thermal stability in cowpea (Ismail and Hall, 1999). The genotypes with high temperature tolerance at flowering and pod set had less electrolyte leakage than those susceptible to high temperature at flowering or at both the stages.

The genes for tolerance to high temperature are linked to genes controlling growth habits in common bean. Shonnard and Gepts (1994) recorded that gene controlling growth habit (determinate or indeterminate) either is linked to factor(s) affecting high temperature tolerance during flower bud formation or has pleiotropic effects. Genotypes also differ in the number and nature of gene action for high temperature tolerance. In snap bean cv. PI297079 a single dominant gene is responsible for tolerance, while in PI151062, two genes with epistatic action confer tolerance. These identified genes in the crops have been successfully used in developing tolerant cultivars to high temperature. Genotypic differences for partitioning and crop growth rate in groundnut were identified by Ntare *et al.* (2001). It thus necessary to establish the genetic basis for variability in heat tolerance based on reproductive traits in the groundnut germplasm, which can than be used in the breeding of heat and drought tolerant cultivars for the areas with climate extremes in SAT.

Pod yield was reduced in genotypes described in Chapter 3, Chapter 5 and Chapter 6 relative to their tolerance to high temperature. Under high temperature, there was no decrease in source (C) or partitioning (p) or flower number (D_r) during the treatment period to account for instantaneous pod yield reduction. To account for this variation, 21 groundnut genotypes were screened for high temperature tolerance. Genotypes were screened for their membrane thermostability (MTS) at 54°C measured as percentage relative injury and for pollen germination and pollen tube growth in temperatures ranging between 10° and 45°C.

The selection of genotypes for the screening study was based on their known tolerance to water stress and high temperature. The genotypes that were well established in the tropics and semi-arid tropics (55-437 grown in sub-Saharan Africa, TMV 2 grown in SAT of India) showed tolerance to high temperature. Genotypes 55-437, TS 32-1, ICGS 11, TMV 2 and ICGV 93277 were grouped (based on PCA analysis) as highly tolerant and genotypes Kadiri 3, ICGV 92116, ICGV 92118 were grouped as highly susceptible, while others were in between. There was no significant correlation between the genotypes for their tolerance to high temperature and water stress. The water stress tolerant genotypes were scattered depicting their varying high temperature tolerance (Fig. 8.4). This study indicates that eventhough water stress and high temperature occur together, the mechanisms operating to induce tolerance to each of these stresses are different.

A moderate correlation was recorded only between MTS and percentage pollen germinated, indicating that membrane disruption due to high temperature reduces pollen germination resulting in failure of fertilisation. Earlier studies have shown that plasmamembrane integrity is associated with pollen fertility (Heslop-Harrison, 1970; Heslop-Harrison *et al.*, 1984) The optimum temperature for both pollen germination and pollen tube growth for genotypes examined in this study ranged from 24° to 37°C indicating the pollen ability of some genotypes to germinate and elongate pollen tubes normally even under high temperature (>34°C).

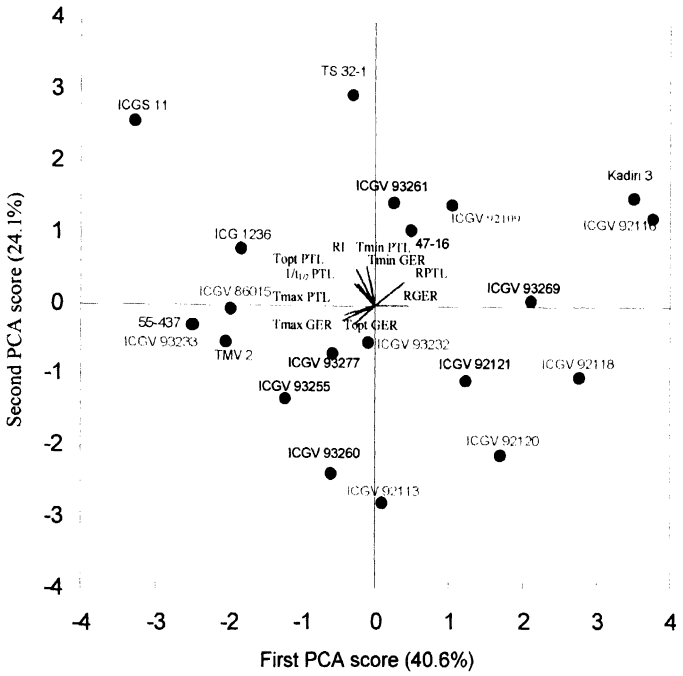


Fig. 8.4 First and second Principal Component Analysis (PCA) scores for the identification of genotype response to high temperature. Genotype with labels in blue are water stress tolerant and those in red are susceptible, tolerance of others is yet to be established. The latent vectors are indicated by red lines showing the direction (angle) and magnitude (length). (RGER- reduction in pollen germination at 40 °C compared to values at optimum temperature; RPTL- reduction in pollen tube length at 40 °C compared to values at optimum temperature; T_{min}, T_{opt} and T_{max} are cardinal temperatures for pollen germination (GER) and pollen tube length (PTL); $1/t_{1/2}$PTL – reciprocal of time to establish 50% of pollen tube length).

It is clear from the research results presented in the thesis that water stress and high temperature decrease pod yields of groundnuts in the semi arid tropics. Hence, breeding for high temperature tolerance into the already existing water stress tolerant groundnut genotypes is essential to improve groundnut yields in the SAT. Before taking up the time consuming and resource intensive breeding programme, it is essential to predict the extent of yield reductions in various groundnut growing regions in India.

A test of PNUTGRO model (Boote *et al.*, 1986; 1988; 1989) to predict water stress effects was carried out using multilocational data from five locations in India (Chapter 7). Simultaneously, the model was also evaluated for its ability to predict the results (biomass, pod yield and pod number) obtained in field study (Chapter 6), i.e. for high temperature and its interaction with water stress. The predictive ability of the model was good under rainfed conditions of SAT, but poor for the irrigated crop performance. Good model performance under water stress conditions is essential as 80% of groundnut cultivated is under rainfed conditions in India. The failure of the model to predict biomass and pod yield under irrigated conditions was mainly due to the SLPF factor (soil fertility factor) that accounts for all the unaccounted variation (soil fertility and biotic stress) in the model. Thus it is essential to improve the nutrient sub-routines and incorporate pest sub-routines to improve the predictive ability of the model under irrigated conditions, as area of cultivated groundnut under irrigation is increasing in India (Fig. 8.1b).

Improvements in the nutrient and pest sub-routines would reduce the need for so much calibration. It would also avoid the aggregation of errors imposed using SLPF. The simplified calibration process will then allow easy coupling of the model to weather generators to predict groundnut yields under current and future climate scenarios with greater accuracy. The model now used for homogeneous plot predictions can be scaled up for regional and national yield predictions (Hansen and Jones, 2000).

The temperature response functions in PNUTGRO for vegetative growth peaks at 28°C and any increase in temperature reduces the vegetative growth (Boote *et al.*, 1998). However, under field conditions vegetative growth continued even at temperatures >40°C. The reasons for this could be due to the fact that sub-routines for photosynthesis and many other physiological processes were adapted from soybean (Boote *et al.*, 1986), a more sensitive crop to high temperature when compared with groundnut (Srinivasan *et al.*, 1996). The model process rates, both chemical and biochemical, are less dynamic than those under field conditions. Mean temperatures over a day are used to simulate the processes. However, the rate of mean temperature is different from mean of the rate over the different temperatures in a day (Allen, 1988). Thus the polynomial temperature sum equations used in models can be replaced by a rate sum, specific for each process to give a more reliable prediction of various growth processes (Tijskens and Verdenius, 2000).

The pod yields predicted by the PNUTGRO model were less than those recorded in the field study. The genotype differences for pod yield observed under field conditions were also not accounted for by the model. This was because the model did not accurately predict pod number at high temperature. The decrease in pod number in model is due to decrease in the carbon pool under high temperature. A decrease in photosynthesis and increase in respiration under high temperature would reduce assimilates available for pod addition. Thus, the addition of pods as new classes or cohorts on a daily basis is hindered. The failure of the model to account for genotype differences to high temperature is due to lack of coefficients, which determine the rate of flowering in the genotypes. Recently Craufurd *et al.* (2000) have shown that the variation in genotype tolerance to high temperature is due to the timing and the initial rate of flowering. The genotypes used in the study have confirmed that differences in pattern and rate of flower production are essential in providing tolerance to high temperature.

The model also lacks the ability to account for the sterility induced under high temperature as pollen fail to fertilise ovary. Hence, the model cannot distinguish between a tolerant and susceptible genotype based on the pollen tolerance identified in this research. The modified bi-linear responses of the pollen to temperature can be incorporated into PNUTGRO to increase its sensitivity to high temperature. Genetic coefficients that account for this mechanism if incorporated will enable the G x E interaction apparent in the models.

The observed flowering patterns of genotypes and pollen response to high temperature need to be incorporated in the model to improve its predictive ability for high temperature effects and climate change scenarios. The rapidly developing understanding of groundnut physiology responses to high temperature should be used to improve the PNUTGRO model through efficient collaboration between physiologists and modellers.

8.1 Future Research

The thesis indicates that base tolerance governs the response of genotypes to high temperature and that there exist differences in tolerance of developmental stages. Hence, studies are required to identify the nature of tolerance and the genes involved in inducing this tolerance. The thesis also shows that different mechanisms operate to induce tolerance to high temperature and water stress in groundnuts. Further experiments are required to understand the interaction between water stress and high temperature, and their combined inheritance.

Research presented in this thesis identifies specific processes (e.g. pollen germination and tube growth) affected by high temperature. Studies are essential to identify the proteins or pathways in determining genotypic variation in tolerance. Studies should then be carried out to identify the genes involved in activating the tolerance proteins or pathways.

Research on basic physiological processes like photosynthesis and respiration response to temperature should be undertaken to define cardinal temperatures

for these processes. The response functions can then be incorporated into the currently existing groundnut models to improve the prediction of growth under future climate scenarios.

Further research is also required to incorporate genetic coefficients for the pattern and rate of flower production into the existing groundnut models identified in this study in order to give a realistic estimate of sink establishment. Process level sensitivity (pollen germination and tube growth) of reproductive components to temperature should also be incorporated into groundnut models, to account for short and extreme high temperature events, for use under predicted climate change scenarios.

The thesis thus highlights the necessity for further research on physiology, growth and development in response to high temperature in groundnuts. This understanding of physiology should then be incorporated in crop models, for a reliable prediction of groundnut yields in areas with high temperatures under future hot dry climates of tropics.

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