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CROP PHYSIOLOGICAL FACTORS INFULENCING GROUNDNUT PRODUCTIVITY

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Groundnut (*Arachis hypogaea L.*) is one of the impor-
tant legume crops of both the tropical and temperate regions of the
world. About 77% of the worlds total groundnut area is in the
semi-arid tropics producing 65% of the total production. Asia
produces 10.9 million tonnes, Africa 5.2 million tonnes, North and
Centrel America 2.0 million tonnes and South America 0.8 million
tonnes.

The average annual production of the leading individual
countries are listed below (Gibbons 1980).

India	6.2 million tonnes
China	2.8
U.S.A.	1.8
Senegal	1.0
Sudan	0.8
Nigeria	0.7

The average yields in the semi-arid tropics (SAT) are low,
usually about 800-900 Kg. ha-1 compared to average yields of

2500 kg. ha-1 in developed countries (Gibbons, 1977). The highest farm yield achieved (9.6 tonnes ha-1) is reported from Zimbabwe (Hildebrand, 1980). Usually the poor realization of the potential yields has been attributed to diseases, pests, and the unreliable rainfall patterns in the SAT.

National average yields are often subject to large temporal and spacial variation for reasons which are not always obvious (Shankara Reddy, 1979). Stabilization of groundnut production by minimising the regional variations in yield has been given greater priority in Senegal than bridging the gap between actual and potential performance (Gautreau and De pins, 1980). Since substantial failures in achieving the yield potential are common, the neglect of groundnut crop physiology in research programs is surprising. These failures must have a physiological explanation and a study of crop physiology would seem basic to any improvement efforts.

Research in groundnut physiology has been limited, starting in the 1950's and since then research efforts have often been discontinuous. During the 1950's work was done in the Netherlands on the effects of environmental factors on groundnut growth using growth chambers. Later in the 1960's Gautreau in Senegal started work on aspects of drought resistance. Williams in Zimbabwe, initiated physiological studies of crop growth in 1970' and in 1973 McCloud began work on aspects of groundnut yield potential at the University of Florida. Krishna Sastry, at Bangalore, started working on drought tolerance machanisms in groundnut in 1975. ICRISAT (at Hyderabad, India) initiated research on groundnut physiology in 1980, This history limits today's knowledge of the crop physiology of groundnuts.

SEED FACTORS AND GERMINATION

A primary requirement in crop production is the establishment of the crop, a process which depends both on the quality of the seed and the environment.

(a) SEED QUALITY

Seed quality, or the factors which determine Seeds' ability to germinate and establish the crop has been the subject of considerable research since this phase of the crop plays such an important role in yield determination. The quality of the seed has been shown to depend on the conditions during it's growth, on the method of curing, and on storage conditions.

Drought during the pod filling stage of the parent crop has been shown to influence seed viability (Pallas et $al.$ 1977) as has calcium deficiency (Cox and Reid, 1964). The effect of drought on seed viability is probably due to induced calcium deficiency (Gillier, 1969).

The method used in curing the preceeding crop influences seed viability mainly by influencing the temperature that the seed reaches and the rate at which moisture is lost. It has been shown that seed has reduced germination percentage when the seed temperature exceeds 49 C (Bailey et $al.$ 1954; and Picket, 1957). Curing methods have, therefore, to limit temperatures of the pods to below this temperature. Curing and storage requirments were investigated for Indian farmers by Rao et al (1975) who showed that curing and storage in gunny sacks in the shade could maintain seed viability through the high summer temperatures. The speed of drying also has an influence on seed quality since slow drying may encourage fungal invasion and too rapid drying may predispose the seeds to testa slippage during shelling and handling (Hildebrand, personal communication).

Seed storage conditions also play an important role in maintaining seed viability with normal principles for seed storage effects operating.

Seed size also has a bearing on crop establishment. Gorbet (1977) reported positive correlations between seed size and plant size, yield, and 100 seed weight of the subsequent crop. Similar

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results have been obtained by Shankara Reddi (personal communication).

Differences in seed sizes in a given parent crop occur because of the non synchronous development of the fruit This results in crops usually never being harvested when 100 percent of the pods have matured, the optimum time for harvest usually being between 40 and 70% maturity of the pods (Metelerkamp and Hildebrand, 1975).

A further source of seed size variation is the different times of pod initiation relative to the changing supply of carbohydrate. The first pods initiated grow faster and achieve a larger final mass than do the last pods initiated (Williams, 1979).

(b) ENVIRONMENTAL EFFECT.

Soil moisture and temperatures are important factors in germination. Mixon (1971) showed that germination will not start below a seed moisture conent of 35% while 50% water content is necessary for radicle emergence and extension. Gautreau (1966) in Senegal has shown that varieties differ in their ability to germinate at different soil water potentials and has devised screening procedures that only varieties able to germinate in unfavourable soil moisture are released for commercial production.

Soil temperature plays an important role in the germination of the groundnut. When the temperature of the top 10 cm of soil was below 18 C, emergence of seedling was uneven and the resulting plant population severely reduced (Mixon *et al.* 1969). High soil temperature may also reduce germination with 54 C being the upper limit for germination (Dickens and Khalsa, 1967).

Depth of sowing inevitably also influences germination largely by influencing the water availability and temperature. Although the groundnut is capable of emerging from great depth (200 mm) there is evidence that seed placement at depths greater

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than 75-100 mm may reduce subsequent yield (Swanevelde, personal communication). Too shallow planting, on the other hand may limit germination since the upper layers of the soil may dry out before radicle emergence and so suspend germination.

THE PHYSIOLOGY OF YIELD

The yield of groundnut is dependent on the rate and duration of crop growth and that proportion of these two components which is utilized for reproductive growth. This section will therefore, examine the factors effecting the rate and duration of growth, the establishment of reproductive structures, and the factors which determine the rate of pod growth.

(a) CROP GROWTH RATES

The crop growth rate (CGR) is dependent on the amount and intensity of energy intercepted and the photosynthetic effeciency of the leaf or canopy.

The major plant determinant of photosynthetic potential is the development and maintenance of photosynthetically active leaf area. Above leaf area indices (LAI) of about of 3 the response to increased leaf area is small but may be significant, and there have been reports of 20% more growth at a LAI of 6 than at LAI of 3 (Fig. 1 from Williams et al, 1979). Complete ground cover in equidistant planting is achieved at a LAI of approximately 3 and once this has occurred the growth rate of the crop depends mainly on other environmental factors since almost all light is intercepted,

The leaf area developed is the product of the leaf initiation rate and the size of individual leaflets. Both these processes are influenced by both genetic and environmental factors. Genetic differences appear to play a secondary role to that of temperature and water stress in leaf area determination. The differences in plant (Fortanier, 1957) and crop responses (Williams, 1975 a) to temperature in a given genotype are relatively large compared to the
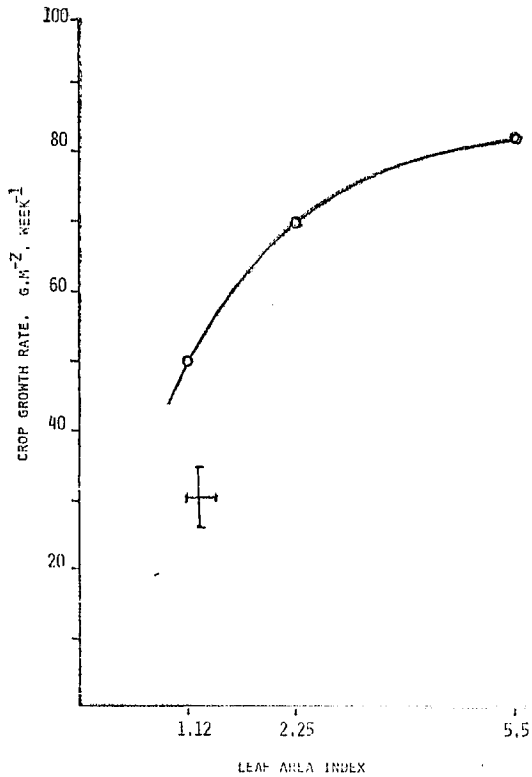
Fig. 1 The effect of leaf area index on crop growth rate of Makulu red groundnuts grown at Salisbury research station, Bars Represent S Es From Williams 1975.

differences occuring between varieties in a given environment (Willlams *et al.* 1975 b; and Duncan *et al* 1978)

Variations over a wide range in population have very little effect on the crop assimilation rate after full light interception is achieved. Populations and plant arrangements usually only vary the time to the achievement of full ground cover, after which environmental variables become the most significant source of variation in carbon assimilation rates.

Diseases play a particularly important role in determining the leaf area of groundnut. There are numerous foliar diseases which can be responsible for defoliation of the crop. The most

serious diseases on a world scale are rust *(Puccinia arachidis)* and *Cercospora* and Cercosporidium leaf spots, In specific localities pathogens such as Aschochyta and Phoma also may play a large role in varying the leaf area of the crop. From a crop physiological point of view there is no evidence to suggest that these diseases influence carbon assimilation in any way other than through modifying the leaf area and light interception patterns of the crop. Diseases may cause many different patterns of defoliation according to :

(i)   the suitability of the climate/microclimate for the spread of disease,

(ii) the inoculum load and

(iii) the host plant resistance.

In regard to disease defoliation, environment and genotype may play an equally important role. When dry atmospheric conditions prevail disease may not influence the leaf area of susceptible varieties. However, in conditions which favour disease development, variations in leaf disease due to genetic resistance/susceptiblity can be substantial.

A factor which plays a role in the maintenace or loss of leaf area in a disease environment is the growth pattern of a variety. Some varieties are able to maintain leaf area for longer by continued leaf growth (Fig. 2) (Williams *et al.,* 1975 b).

Water supply or water stress influences carbon assimilation in two ways. In the short term, the occurence of water stress reduce the photosynthesis of the leaves by decreasing stomatal apertures. Bhagsari and Schepers (1976) related detached leaf photosynthesis to relative leaf water content and concluded that there were only small differences among cultivars and that the response of photosynthesis to water stress was not different from that of other plants. Chen and Chang (1972) (quoted by Krishna Sastry, 1979) have reported no decrease in crop photosynthesis between field capacity and 60%
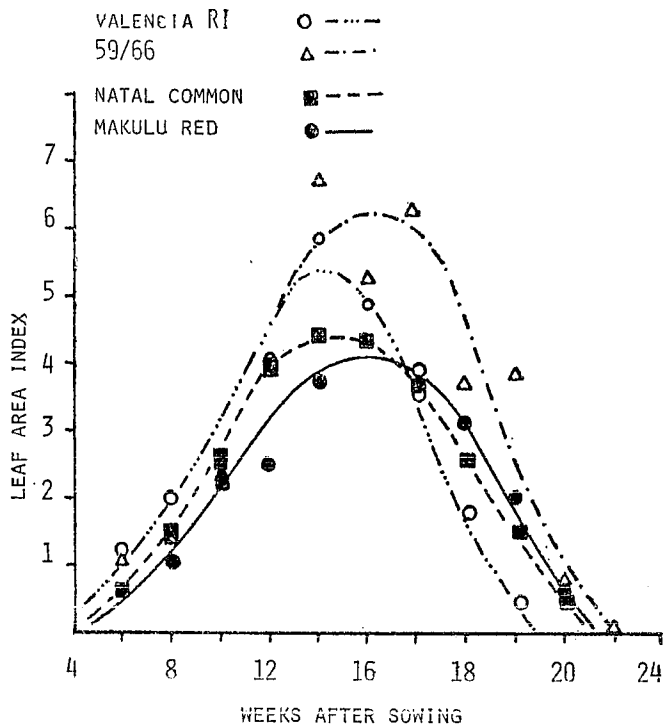
Fig. 2. Changes with time in the leaf Area Indices of four groundnut cultivars grown at Salisbury research station From Williams *et al*, 1956.

depletion of the available soil moisture, but through this range of soil moisture there is not likely to have been any plant water stress.

Water stress has a larger influence on the development of leaf area particularly during the first half of crop growth. No descriptions of the leaf area modification in response to water stress have been published for groundnut but it is clear that there may be substantial (Rao and Williams, unpublished data). Duration and timing of the stress may be responsible for considerable reduction in carbon assimilation.

Although there is little published information, nutrient deficiencies influence the rate of crop carbon assimilation of groundnuts in the same way as in other crops; by both influencing

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the rate of photosynthesis of individual leaves and the leaf area achieved. The leaf area may be influenced directly or indirectly by the shortage of nutrients. Direct effects are manifest in limitations to leaf area establishment or by increased senescence while the indirect effects are the result of decreased photosynthesis limiting the carbon supply for the growth of leaves.

Temperature influences the carbon assimilation of the crop by varying the leaf area establishment. Fortanier (1957) found that from 20 C to 35 C the rate of leaf initiation increased with increased temperatures. However, the area of individual leaves was greatest at 30 C (day temp.), temperatures above this resulting in smaller leaves. Williams et al, (1975 a) found that in the crop situation, at a standard population (45x15 cm) a mean temperature of 23 C resulted in the developmet of a L.A.I. of 7 while at 18 C the L.A.I. achieved was only 3 (Fig. 3). These differences were due to the effect of temperature on the rate of leaf growth. The crop growth rates at these temperatures were 140 and 90 g m-2 week-1 (Fig.4) respectively.

The groundnut has a C 3 photosynthesis mechanism which means that photorespiration does occur. However, the rates of photosynthesis (130 ng CO2 cm-2s-1 at 1800 mE m-2s-1) are as high as the best found in other C 3 plants (Rawson and Constable, 1980) and canopies are not light saturated below full sunlight (Pallas and Samish, 1974) There is some evidence that single leaves of varieties may have different photosynthetic rates (Pallas, 1981) but this may have little significance to crop growth since no major differences in crop growth rates have been found to exist between varieties (Duncan et al, 1978).

(b) DURATION AND DEVELOPMENT.

The most important factors which influence the development of the groundnut are temperature, genetic potential, disease and water stress. The initiation of stages is predictable from the first two
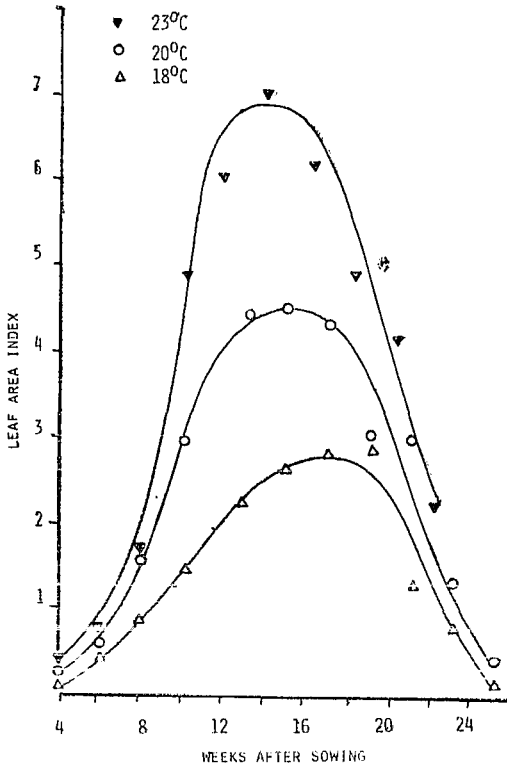
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Fig. 3. Changes with time in the leaf area indices of groundnut Cv makulu red grown at sites with three mean temperatures, from Williams *et al.,* 1975a,

factors. However, the control of the termination of pheneological stages is very much more complex because of the indeterminate habit of the crop.

Temperature plays a major role in varying the time taken to initiate and open the first flowers. However, subsequent development appears to be subject to many other influences and only in controlled environments does the subsequent development related well to the temperature conditions (Campbell, 1980). Emery *et al.,* (1969) developed a heat unit index which was able to account for variations (in calendar time) from sowing to first flowers. However, heat units have been examined in terms of time to maturity in field
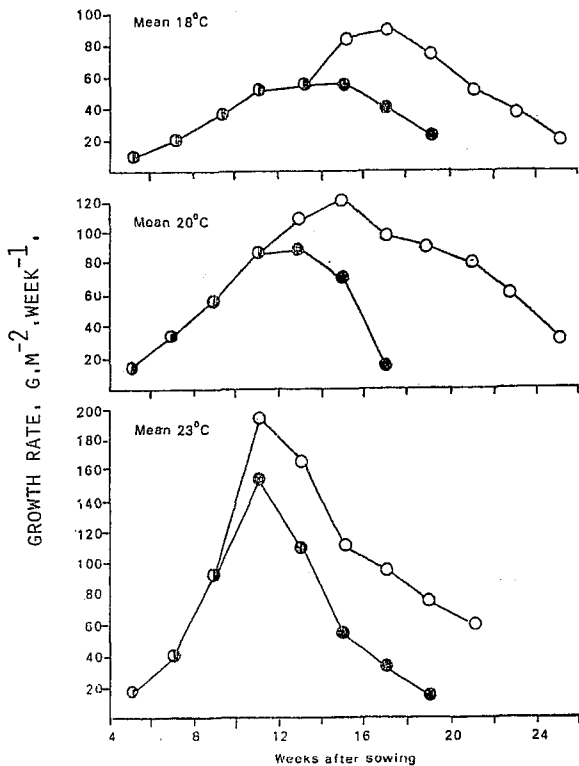
Fig. 4. Changes with time in crop growth rate (o) and vegetative component growth rate (●) of groundnut Cv makulu red grown at three sites with different mean temperatures from Williams *et al*, 1975a,

conditions (Mills 1964) and have proved to be unreliable, due to modifications by other factors not related to the temperature environment. Genetics also plays a major role in varying the development patterns of the groundnut. One of the major differences between the subspecies hypogaea and fastigiata is their different rates of development. However, there is no evidence of a genotype x temperature interaction in the development of groundnuts from different subspecies when grown across a range of temperature conditions.

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Stresses may operate to modify development in two directions depending on time, type and severity of the stress. Stresses which are known to influence development are water and disease.

Early water stress generally suspends development of the crop in that time to the opening of the first flowers may be increased. However, this water stress effect may only influence the opening of flowers, the initiation may be unaltered (Williams, unpublished data).

Water stress during reproductive growth may result in slower or quicker achievement of maturity depending on the time of the onset of stress. Water stress early in this phase will delay maturity by preventing reproductive development while later stress will hasten the achievement of maturity by preventing the initiation of pods, and (because of shortage of assimilate) speed the achievement of maturity of the last initiated pods (Williams 1979 b).

Diseases which influence development most commonly are the leaf diseases and invariably these influence maturity by decreasing the carbon assimilation. There are no known reports of disease altering the timing of other developmental processes although the virus diseases, in particular Rosette may prevent reproductive development.

(C) THE ESTABLISHMENT OF REPRODUCTIVE STRUCTURES

There are four stages of reproductive establishment which are readily discernible, flowering, peg initiation and elongation, pod initiation and kernel initiation Each of these processes are subject to environmental and genetic effects which may alter the rate at which a crop carries them out (Fig. 5 and 6).

1. FLOWER PRODUCTION

Flowering has been the subject of much research and many of the factors which control this process have been examined. Flower production by the groundnut usually occurs at a rate, and in numbers, well in excess of the production of the subsequent structures. Both environmental and internal factors influence
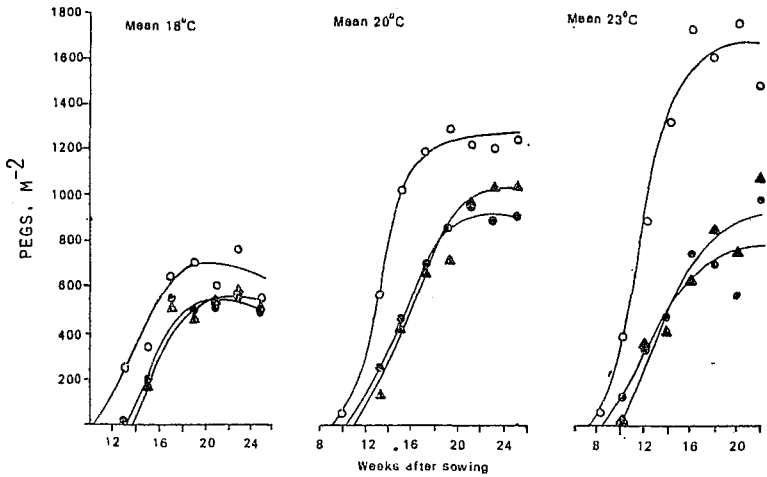
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Fig. 5. Changes with time in the numbers of pegs (o), pods (•) and kernels (▲) present in makulu red crops grown at sites with different average temperatures, from Williams *et al.* 1975a.

flowering, apparently through their effect on the supply of photosynthetic products necessary for flowering (Wood, 1968).

The rate of flowering is influenced by the environmental conditions two to three days previously, temperature having a major role in determining the rate of flowering (Nicholaides *et. al.* 1969). The opening of flowers has been well related to mean temperature (Fortanier, 1957) and to a heat unit value (Wood, 1968). Bolhuis and De Groot (1959) and De Beer (1963) found that most flower production occurred at the temperatures which allowed most vegetative growth. Williams ((1979 a) varied flower production by light treatments which increased or decreased photosynthesis, confirming the role of carbon supply in determining flower production.

2. PEG INITIATION AND ELONGATION

Not a great deal of attention has been paid to this reproductive process or to the factors which influence it. Many authors have drawn attention to the numbers of flowers which fail
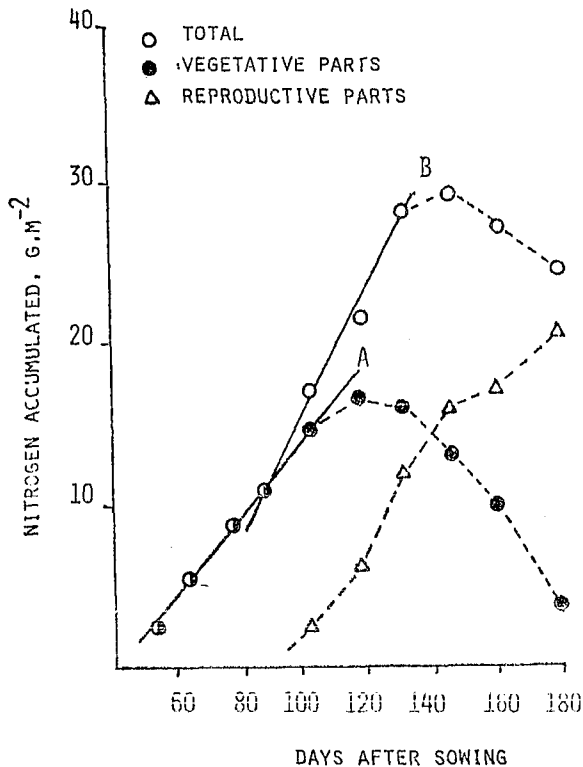
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Fig. 6. Changes with time in the pod number of four groundnut cultivars grown at Salisbury research sation. From Williams *et al.,* 1975b.

to produce pegs but generally the physiological reasons for these failures have not been sought. Circumstances which can result in variable or low peg to flower ratios are :—

(i) Flowering may continue after peg initiation ceases. This response seems to occur mostly in the varieties with low yield potential. Both flowering and peg initiation have been shown to be influenced by the availability of photosynthate and it seems that flowering can continue at levels of photosynthate supply which prevent subsequent peg initiation.

(ii) Sudden variations in the environment which allow suddenly increased assimilation (e. g. the release of water stress) can cause

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the plant to flower profusely when a normal level of efficiency of those flowers would produce more fruits than the crop could reasonably expect to develop.

(iii) Varieties may differ substantially in the percentage of flowers which develop pegs or pods after the effects described above have been accounted for, variations of between 13 and 50% in the success rate of flowers in forming pegs may occur between varieties (Williams *et. al.* 1975 b). These variations in efficiency have not been further investigated but those varieties with limited flower production generally have smaller flower to pod ratios (Williams *et al,* 1975 b).

It appears that peg initiation is also influenced by the availability of photosynthate; many environmental factors therefore influence the process through their effect on photosynthesis. The total peg initiation has been found to increase as temperature increased from a mean 19 to 23 C (Williams *et. al,* 1975 a) (See Fig. 5). Peg initiation has also been shown to be influenced by photoperiod in some genotypes (Wynne *et. al.,* 1973; and Emery *et. al,* 1981) This phenomenon may vary the yield achieved by a variety and it probably contributes to the variations in varietal adaptation across regions. The mechanism involved is at present not fully understood

Peg elongation is an aspect of the crop which has received very little research attention although the inabiliy of the pegs to reach the ground is a factor in reproductive efficiency (Williams *et al* 1975 a). Only one report is known concerning environmental factors which vary the rate of peg extension. Lee *et al..* (1972), found that relative humidity, water stress and the stage of reproductive growth influenced peg elongation rates.

3. POD INITIATION

Pod initiation depends on both internal and external factors. The supply of photosynthates, genetic factors and independent environmental effects are known to be involved.

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Basic to the rate at which pods may be initiated is the rate at which pegs are initiated and penetrate the soil surface. All the factors which influence flower and peg production also influence the rate of pod initiation.

Several researchers have investigated the stimuli necessary for the pegs to initiate pod expansion (Zamski and Ziv, 1976; and Shenk, 1961). For practical purposes there seems little alternative to the peg penetrating the ground and so achieving the mechanical and environmental stimuli necessary for pod initiation. This means that any factor which may prevent the pegs from reaching or penetrating the soil surface will decrease the success rate of the pegs. Those factors which may do this have been mentioned in the section on peg elongation.

Plant morphology may have a large impact on the peg/pod efficiency. Runner and short statured plants may have very high peg to pod efficiencies. In varieties with an upright growth habit peg efficiency decreased in a linear fashion for increased stem growth (Williams et. al., 1975 a).

External factors which effect photosynthetic activity, particularly those which occur before pod initiation starts appear to have an effect on the pod initiation rate (Williams et al., 1971) as does temperature (Williams et al,. 1975 a). Williams et al, (1976) found that defoliation treatments reduced crop growth rates and effected a proportional effect on the pod initiation rates.

However, internal competition for photosynthates caused by the existing pods appears to have little influence on the rate of pod initiation in no—stress conditions, through a wide range of pod loads the rates of pod initiation remain constant (Fig 6). Internal competition varies total pod numbers by changing the duration of the initiation phase (Duncan et al, 1978, and Williams 1978).

Water stress may influence pod initiation rates indirectly

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through the effect of stress on photosynthesis and peg elongation. These effects, although not well documented, seem reasonable from a physiological view point. In addition to these effects water stress may influence pod initiation by the physical hardness of the soil surface preventing peg penetration (Shankara Reddi, unpublished data).
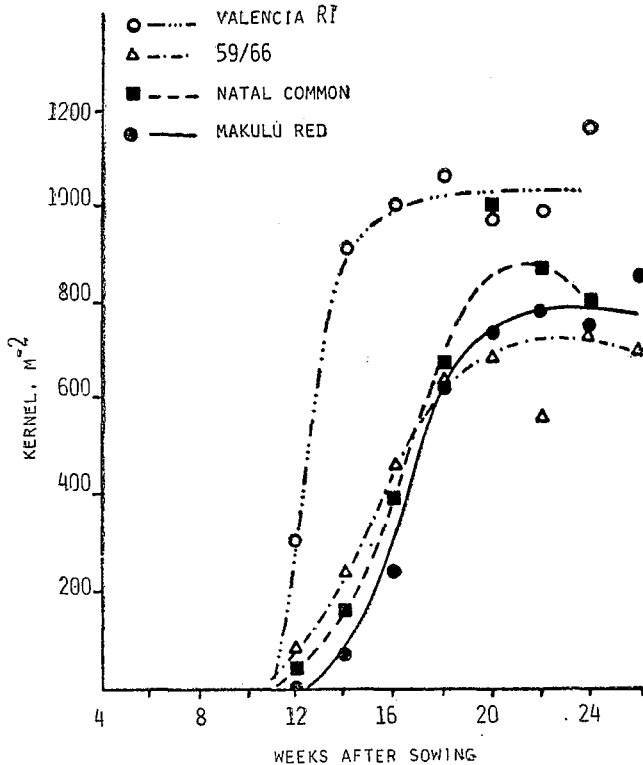

Fig. 7. Changes with time in the kernel number of four groundnut cultivars grown at salisbury research Station. From Williams 1975b.

Kernel production is dependent on pod initiation and those genetic and environmental factors which determine the numbers of kernels in each pod. The differences in kernel initiation between some varieties (Fig. 7) have been described by Williams *et al.* (1975 b) and the number of seeds per pod may be as important as the pod set pattern in determining sink establishment.

The availability of calcium in the soil plays a major role in determining the kernel initiation pattern of a crop. Unsufficient $Ca++$ uptake (due to either low soil $Ca++$ status or inadequate soil water in the pod zone can cause the zygote to abort (Bledsoe and Harris, 1950) so reducing kernel establishment.

Kernel initiation rates are also influenced by the availability of photosynthate which appears to influence the proportion of the potential kernels which are able to develop. In this phase of reproductive initiation the internal competition of already existing peds does influence the rate of kernel initiation by the crop (Williams, 1978). Although this phenomenon is difficult to measure satisfactorily it is apparent from examinations of the numbers of seeds per ped in peds initiated from different stages of the pod setting phase.

(d) REPRODUCTIVE EFFICIENCY

Reproductive efficiency or the proportion of flowers and subsequent pegs which result in pods is discussed as a separate issue since this topic has attracted a substantial amount of interest by scientists from outside the physiological discipline This interest has resulted in numerous reports of the varying reproductive efficiency of the crop and the gains in yield potential to be realized in improving this efficiency. Many of these investigations of reproductive efficiency have been based on flower counts and determination of peg and pod numbers at maturity (Goldin and Har-Tzook, 1966; Har-Tzook and Goldin, 1967; Bolhuis, 1958; De Beer, 1963).

However, these reports have provided little additional understanding of the subject and no scientific basis for improvement strategies Within varieties where there is little further carbohydrate available for increased pod growth there is still substantial over production of flowers. The reasons for the failures of these researchers to contribute to information stems from the lack of serial growth measurements and the fact that a change in reproductive efficiencies may occur with time (Martin and Bilquez, 1962).

An exception to this has been the work on photoperiodic effects (Emery *et al,*. 1981, Wynne, *et al,*. 1973) where reproductive efficiency changes have been shown to have a major effect on yield potential. These effects can be expected to have little significance within varieties adapted to the region.

Investigations of crop growth by growth analysis tenchniques have provided the basis for the current understanding of reproductive efficiency and the factors which influence it. This work by McCloud in Florida and Williams in Zimbabwe apprcached the problem from different points of view although there is still some uncertainity as to some of the mechanisms involved, a substantial improvement in the understanding of this phenomenon has been achieved.

Reproductive efficiency has been shown to be a highly flexible process with changes in the success rate of each component process to adjust the assimilate requirements of the reproductive sink to the total assimilate available (Williams, 1979 b; and Hugdens and McCloud, 1974). This mechanism allows the crop to adjust to the variations of the climate and ensure that some viable seed is produced.

(e) INDIVIDUAL POD GROWTH RATES

The growth of individual fruit has only been studied by only a few researchers, whose papers show that individual pods from different varieties may vary both in the rate and duration of growth. Shenk (1961) found that the differences in the final size of pods from Dixie Spanish and Virginia 67 Bunch occurred because although they had similar pcd grcwth rates the duration of pod growth differed. Williams and Alison (1978) showed varietal differences in both the rate and duration of pod and kernel growth.

Soil temperature has also been shown to influence the individual pod growth rates with the highest growth rates being between 30 C and 34 C ₍Fig. 8 from Dreyer, 1980). The competition
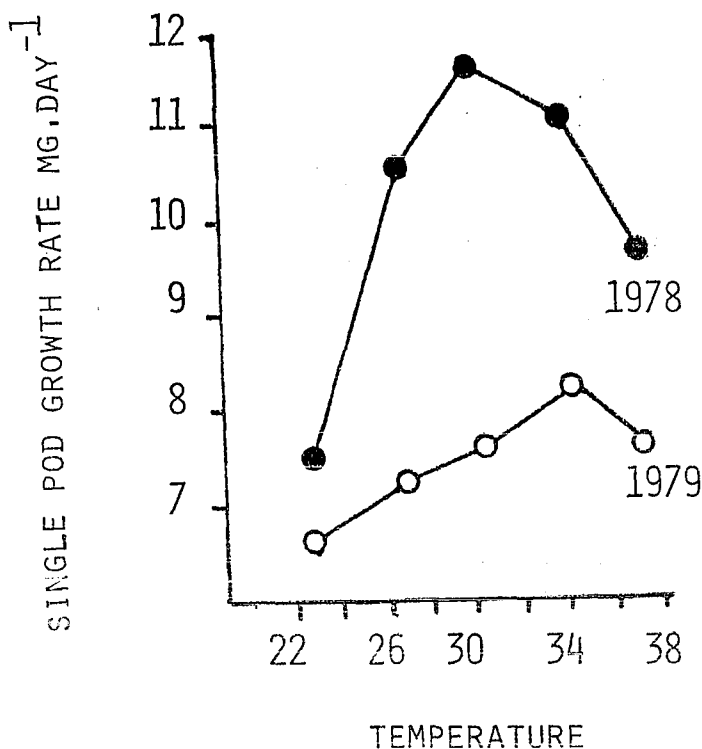
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Fig. 8 : The influence of pod zone temperatures on single pod
growth rate From Dreyer 1980.

of other pods may decrease pod growth rate and duration (Williams
1979b) or not (Boote, 1976) depending on the variety involved.

(f) GROWTH DISTRIBUTION

(I) BETWEEN VEGETATIVE AND REPRODUCTIVE STRUCTURES

It is clear that the yield is strongly influecend by that
proportion of the total growth which is used for reproductive
purposes. It is less clear, however which factors control this
distribution. The date presented to date shows that reproductive
efficiency is influenced by the supply of carbohydrate but also that
the proportion of growth available for reproductive growth can be
influenced by the reproductive sink established.

McCloud and his colleagues in Florida found that for their environment the proportion of total growth which was used for pod growth was constant for a variety and that varietal yield differences were due to differences in this 'partition factor' rather than differences in total growth (Duncan et al,1978). Dreyer (1980), and Dreyer et al,, (1981) tested this hypothesis of a constant partition factor by modifying the temperature of the pod zone but their interpretation is controversial since the same data can be used to show that the partition factor can be modified by the differences in pod zone temperature (Williams unpublished manuscript).

(2) ASSIMILATE SUPPLY TO THE NODULES

Nitrogen influences yield in several ways, the most obvious ones being in determining the leaf area and carbon assimilation. However, as the supply of N is by symbiotic fixation the feedback of carbohydrates to the nodules and the rates of N fixation in response of this is of great interest and significance to the achievement of yield. This is important since photosynthate is a major limitation to N fixation (Nambiar et al, 1980) and upto 1/3 of all carbon products in legumes may be directed to the nodules of legumes (Pate, 1976). In most legumes this supply to the nodules is limited by competition for assimilates from the developing fruit. Groundnuts apparently have a different response since N assimilation by the crop can be at its greatest rate during reproductive growth (Fig. 9), and total nonstructural carbohydrate levels can be greatest in the roots during this time (Williams, 1979 a) . This nitrogen fixation response is apparent only in some varieties, and has been associated with high yield potential (Williams, 1979 a). It seems that once stem growth has stopped, competition by the pods limits N fixations, but not before. Apparently, the nodules are a more competitive sink than the stems (Williams, 1979 b).
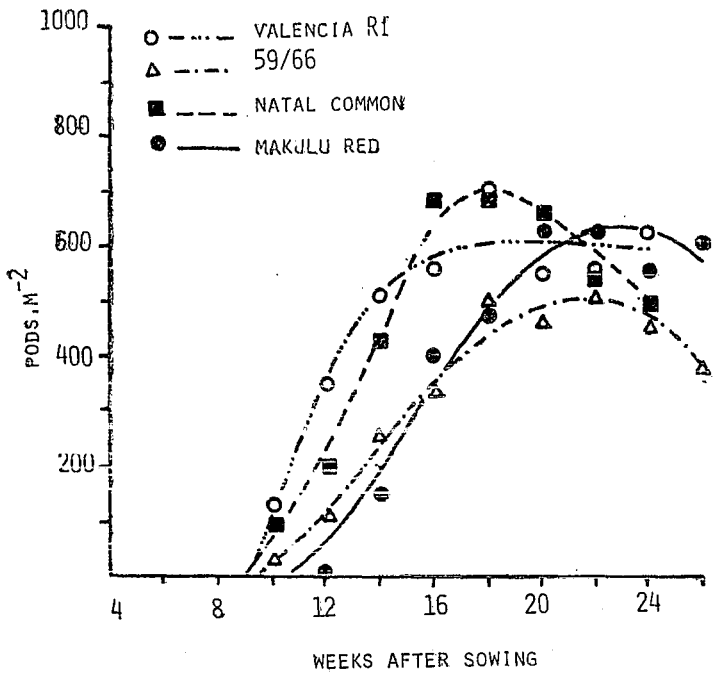
Fig. 9. Changes with time in the nitrogen accumulated in the total
crop and in vegetative and reproductive components of
egret groundnuts.

A (VEGETATIVE N) =

-9.87 ($+/-$ 0.54) $+$ 0.241 ($+/-$ 0.007)

B (TOTAL N AFTER REPRODUCTIVE GROWTH STARTS) =

-21.38 ($+/-$ 3.01) $+$ 0.373 ($+/-$ 0.027)

From Williams 1979a,

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