Genetic Manipulation For Improving Crop Production
In Stress Environments.
A Physiologists View Point

J.H. Williams
Principal Groundnut Physiologist
ICRISAT
Patancheru P.O.
Andhra Pradesh 502 324

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Stress may be defined for the purposes of this paper as a condition within a crop or plant which reduces growth. Many factors may cause crop stress, however the most common stresses encountered by crops are drought, nutrient, temperature, insect and disease.

That stress plays a major role in the crop production of the world is indicated by the great differences in the yields achieved in most crops compared with the biological yield potentials of those same crops. In groundnuts a crop growth rate of 25 g/m^2 day has been recorded in India between January and March and 18 g/m^2 day has been recorded in the monsoon season. This suggests that India's average groundnut yield of 800 kg/ha could be produced in one week of growth by a variety with high partitioning of assimilates to reproductive components. These results suggest that stress of various kinds is producing an 80 percent decrease in yield performance. This is confirmed by the fact that at ICRISAT we have been able to achieve yields of 6.8 t/ha of pods in replicated trials during the monsoon season. It is very clear from this analysis that stresses are a major limitation to groundnut production. This is also probably true of most of the world's crops. Although environmental manipulations to reduce this stress would bring large changes in production, they are not always possible and the question which we have to address is how much improvement can be achieved by genetic manipulation within this stress environment and how can this be done most efficiently.

The green revolutions in wheat and rice have been hailed

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as a victory for breeding. In reality, these impressive changes in productivity are as much attributable to environmental manipulation as to breeding: they have involved the removal by man of limiting environmental factors and a marked decrease in the occurrence of stress, particularly nutrient and water stresses. Without these environmental changes the genetic manipulation would have achieved only limited changes in productivity. When breeding for a given improved 'package' of environmental circumstances, the task of selecting genetic characteristics better adapted to these conditions is relatively easy. The rapid advances in wheat and rice are witness to this phenomenon. However, once a reasonable level of genetic adaptation is achieved progress becomes slower, the gains possible diminish and hence the challenge to progress increases.

Viewed in the sense that the landraces are well adapted (since they are the result of long term continuous selection for the environment) the challenge of improving on these without simultaneous changes in the production environment must not be under estimated. At all times the possibilities opened up by changed management need to be considered. The only occasions where rapid improvement seems possible without modified management is where either the original germplasm base was narrow; or where there has been a rapid change in the environment, for instance a new disease, changed rainfall or soil fertility.

Three factors are essential to the plant breeders' prospects of progress. First, there is his understanding of the limiting factors that he is dealing with, then the existence and availability of genetic diversity for responses to these factors, and thirdly his ability to identify this diversity. These three considerations will allow him to decide whether escape, tolerance or resistance will be the best opportunity of improving yield in the farmers circumstances. The disciplines of pathology, physiology, agro-meteorology and economics play an important role in all these aspects and, in the event of these supportive sciences not being available, the breeder has to fill these roles on his own.

1. THE UNDERSTANDING CROP PHYSIOLOGY AND STRESS ENVIRONMENTS :

The factors which determine productivity and how stress modifies these needs to be described as a basis for further discussion on ways of overcoming these stresses to allow greater productivity. The primary components of crop productivity are the amount and intensity of radiation intercepted, the duration of this process and the plant's ability to convert radiant energy to chemical energy.

The amount of radiation intercepted by the canopy of a crop in non-stress circumstances is well related to the dry matter accumulated. This relationship has been observed for most crops studies, for example barley (Biscoe, Scott and Monteith, 1975). The intensity of light incident on the leaves within a crop is largely dependent on the total area and the orientation of leaves. Differences in the distribution of the light over the leaves may result in differences in the efficiency of light utilization but the basic relationship for one particular crop type seems to hold good.

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However, as growth is dependent on the amount of radiation intercepted so is water consumption. Indeed one of the major environmental determinants of evapotranspiration is the amount of incoming radiation (Monteith, 1973). Inherent in most models predicting water use by a crop is some method of accounting for the amount of radiation intercepted by the crop. Because of this double role of radiation in determining growth and transpiration it is hardly surprising that growth is closely related to water use.

The syndrome of drought stress occurs when water supply can no longer keep pace with the demand created by the radiation intercepted and transpiration and growth decrease or stop, primarily because the stomata close to decrease water vapour loss and so limiting the diffusion of CO_2 into the leaf. With the closure of stomata the leaf has to dissipate the energy intercepted by means other than evaporative cooling. To compensate for the loss of evaporative cooling the leaf temperature has to rise until the energy lost by radiation and convection equals that no longer being lost due to evaporation. Leaf temperature may rise to $10^{o}C$ above the air temperature and temperature stress may become an important component of drought stress.

When water is not available to the crop in sufficient amounts the supply of nutrients may also be restricted or interferred with, introducing nutrient stress as the third component of drought stress.

The duration and development of a crop is determined by the interaction of genetical factors and environment. In most

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crops the environmental factors which influence development are temperature and photoperiod.

Photoperiod alters duration by inducing flowering when a given photoperiod requirement is satisfied. This response to photoperiod provides a major adaptative mechanism to synchronize flowering with a calender date rather than a thermal time date after sowing, an ability which can be exploited to advantage by the breeder in certain environments.

However, despite the photoperiod effects on reproductive initiation, temperature is the environmental factor which plays the largest role in the development of a crop from sowing to maturity. The initiation and expansion of leaves, nodes and internodes and the transition from vegetative to reproductive phases (in many crops) are some of the processes which are regulated by temperature. The regulatory effect of temperature on development has been well established and, with adjustments for the base temperature, physiological development is often linearly related to thermal time (heat units).

When drought stress occurs, although the assimilation of carbon is decreased or halted by the shortage of water, the developmental processes may not be retarded, rather they may be accelerated because the temperature of the stressed tissue may increase when subjected to a radiation load. Since the thermal time life cycle is not suspended when the stress occurs the plant may reach the end of its life cycle while little growth has occurred, hence the decreases in yield from drought.

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The amount of radiation intercepted can also influence yields achieved in other stress circumstances, particularly in the case of foliar diseases. In groundnuts when disease stress is serious the yield of a variety may be linearly related to the amount of leaf remaining at the end of the season (Fig.1). However, due to the relationship between energy intercepted and water use, defoliation may also be a major adaptive advantage in drought conditions. In Nigeria, Zimbabwe and Australia attempts to reduce defoliation stress by fungicidal sprays has decreased yields of groundnuts grown in droughty conditions (MacDonald D; Hildbrand, G.L. : personal communications). A similar situation may arise in the interaction of nutrient and water stress. Nutrient stress may be beneficial in limiting the leaf area developed to allow a crop to produce grain with a limited water supply (Willey, R.W. : personal communication).

The strategies that the breeder must adopt depend on the nature of the stress environment for which he has to improve yield, therefore he should have a good understanding of this environment. For drought stress the problem is indeed complex considering the variable nature of the environment. There are several parameters that can be isolated from meteorological data which could help the breeder. In this the agricultural meteorologist can play a major role in assisting the breeder define the nature and probabilities of variation in the season. At present only partial and inadequate information is generally available for these characteristics. The important aspects are the mean and variability of the start and end of

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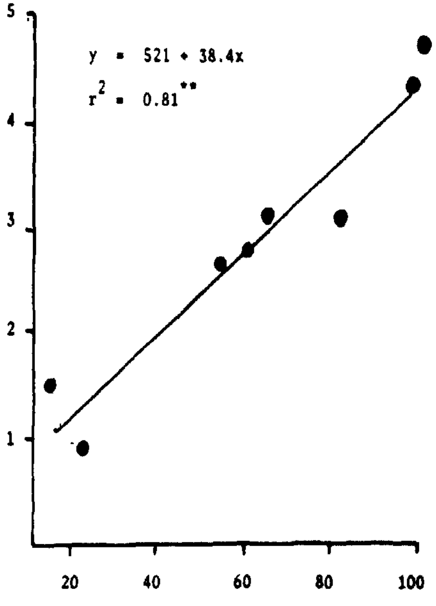

Fig. 1 : The relationship between yield and percentage remaining green leaf at maturity for Robut 33-1. (Subrahmaniam et. al. in preparation).

moisture availability and probabilities of adequate moisture between these dates. Knowledge of these attributes of the environment allow the breeder to decide on the amounts of stress escape,resistance and tolerance that are possible.

The method of calculation normally adopted is to utilize long term means of rainfall and evaporation and determine when and for how long the daily and weekly rainfall exceeds some proportion of the evaporation. This method of season analysis masks to a large extent the variability inherent within the season and for decisions on breeding options is likely to result in wasted effort.

For instance, a season length of 90 consequetive days when rainfall equals or exceeds evaporation in each year may be assessed very differently when analysed using long term mean data if there is a large variability in the date of start of the season.

Variability in the start and end of the season introduces important considerations for the breeder. The decision on whether to utilize photosensitivity or not probably depends on the nature of this variability. If the start of the season may occur over a wide calendar period and the end of the season varies little or independently of the season start. Photo insensitive crops may stand a greater chance of rain after maturity than a photo sensitive crop which would flower at a calender date regardless of the sowing date.

A good example of the dangers of not considering this end of season variability is provided by the sorghum hybrids

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which have been selected for early flowering as a drought escape mechanism. These lines are often subjected to rain after maturity and the grain moulds have become a major problem in their cultivation. The breeder should be sure that he is not going to develop one problem while attempting to solve another. Short season varieties need to have increased resistance to wet weather after maturity, or there must be changes in managerial capacity on the part of the farmer to allow harvest regardless of the weather. Where the season length is reliable regardless of the time of start the decision on desired season length to minimize the occurrence of stress is quite simple. However, variability in season length is not the norm in many of the world's stress environments.

Reducing the season length requirement of a crop will increase the probabilities of growth (particularly of grain) co-inciding with available water but this stragey will also; a) increase the chances of post maturity loss in those seasons when the rainfall duration exceeds that of the crop; b) decrease the yield potential since the duration of radiation interception is decreased, and the grain growth phase may be a constant proportion of the crops life and decreased accordingly; c) increased drought susceptibility in the sense that a drought of a given length represents a larger proportion of the crops life and will accordingly have a larger impact.

2. THE EXISTENCE OF VARIABILITY FOR STRESS RESPONSES :

The second requirement for progress by genetic manipulation is the existence of variability within the germplasm.

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Naturally occuring mutations occur with given frequencies so it is always possible to find variation which may impart advantage in stress environments. However the survival of these mutations within the population depends on whether they impart a benefit to the species within that environment or not.

Where the advantage in a stress environment is controlled by a single locus it is possible for these mutants to exist within the population at low frequencies providing they have not deleterious effects. This situation of a single gene factor benefit is most likely where the stress involved is biological i.e. disease or pests. However, where the variability in response to stress is dependent on growth characteristics it seems likely that multigenic control would be involved and for many genes to be accumulated within a genetic line this would require that particular stress to have been a feature of the crop's evolutionary history.

The increased germplasm collections being made now are of great value to potential progress in stress environments, as they are making available to scientists the full range of material that has developed over the ages. For some attributes the existence of genetic variability is well documented, however for others the evidence does not exist and indeed the characteristics which may impart an advantage are often not easily identified. However the existence of variability can be established by the same methods that are used to identify desireable attributes as discussed in the next section.

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IDENTIFICATION OF DESIRED ATTRIBUTES :

The third aspect that has to be considered in manipulating for increased yield in stress environments is the identification of desireable attributes within the germplasm, the combination of these by crossing and the identification of desired combinations from amongst the segregating progenies.

The theoretical considerations which determine yield may be used as a basis to develop methods of identification. Increased yield can be expected from attributes which increase the amount of light intercepted and the efficiency of light utilization; increase the amount of water available to the plant or conversely decrease the utilization of water. Another attribute which may be significant in the case of severe, intermittant stress is the ability to recover rapidly and function in a stop-start manner.

How does one identify characteristics which will achieve one or many of these objectives, bearing in mind the requirements of a breeding program, the multigenic inheritance of many of the characters, particularly the large amounts of material which are involved and the consequent need to be able to identify characteristics as easily as possible.

Characteristics which result in increased light interception are usually easily identified, particularly in the case of foliar disease stress. The amount of light intercepted at any time in the season can be visually estimated by ground cover estimations, which the proportion of active green leaf can also be estimated with relative ease. However, it is important that even disease pressure occurs on all varieties. The development and management of disease nurseries and the use of infector rows is well documented, and for groundnuts good sources of resistance have been identified to overcome this type of stress (Subramanyam et. al, 1980 and in press). This procedure of disease nurseries can be used to identify both parents from the germplasm and valuable segregants from populations.

The identification of characteristics which improve the efficiency of light utilization may be more difficult because the gains, even in non-stress environments, are likely to be small and the costs of working on this problem are very substantial.

Improving the amount of available water and the efficiency of its use can be achieved in several ways. The exploitation of a greater soil volume by deeper roots and the extraction of water to lower water potentials are possible methods of achieving this Evidence of genetic differences in the root number at depth have been provided for groundnuts (Ketring and Jordan, 1981) while in other crops, for example wheat (Morgan 1980), osmotic adjustment allows for growth in dryer soils and possibly for greater extraction of water from the soil. Other methods of increasing crop growth in the face of water shortage are the suspension of or a decrease in the rate of development, and the ability to continue producing dry matter despite decreased water potentials. These attributes although valuable cannot be

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measured with ease and indirect methods would seem the only option.

Another factor which is significant in drought stress in groundnut is the ability to decrease the radiation intercepted by the process of leaf folding. This attribute has particular significance as it may protect the plant from tissue destruction due to high temperature and conserve soil moisture.

Yield potential in good environments and performance in stress environments are often inversely related because of a number of factors. A part of this inverse relationship is due to the fact that high yield potential often leaves very little energy available for the plant to utilize in overcoming the stress. For example, greater root growth requires carbohydrates at the expense of grain growth, but as the grain is usually the dominant sink the only way root growth is possible during grain growth is for the grain sink to be such that some surplus remains available after the requirements of the grain.

Although the reason is still obscure, this phenomena often applies to disease resistances. An example is found in groundnuts where in the presence of a complex of leaf spot (Cercosporidium personatum) and rust (Puccinia archidis) the level of resistance possible decreased progressively as the yield potential increased. (Fig.2 Subramanyam et. al. in preparation).

However, as yield potential may be of little consequence because of the over riding effect of stress it is still worthwhile exploiting resistances. The most important fact to be remembered is that inverse relationships can exist

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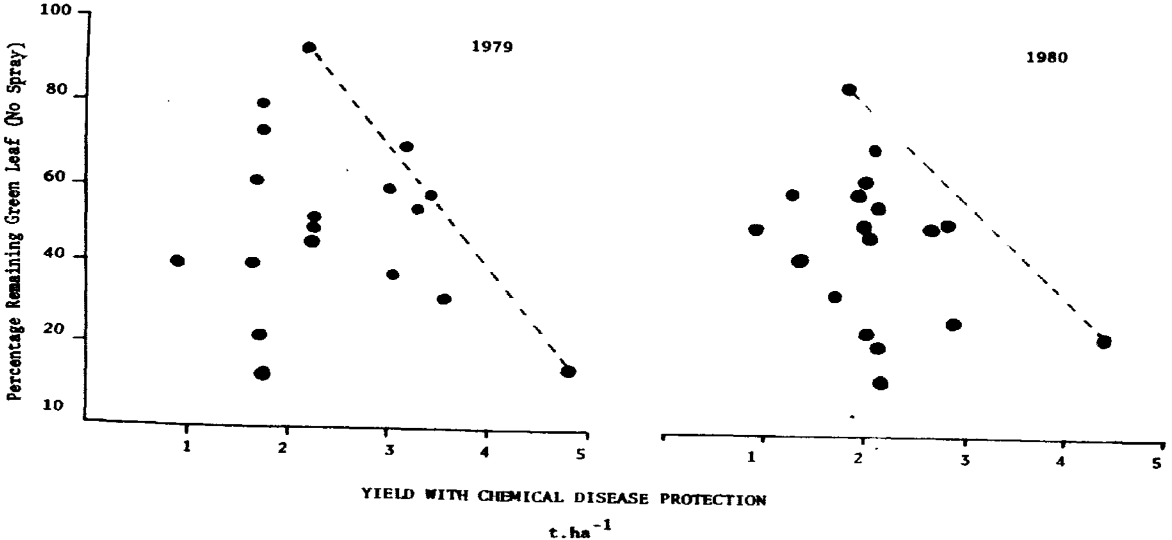

Fig. 2: The relationship between resistance to *foliar diseases* and *yield* potential within groundnuts

and that selection in better environments than the actual production environment can be futile.

The identification of single desired characteristics is often difficult and not practicable for breeding purposes. How can one select for improved performance in stress, particularly when the desired traits are not likely to be simply inherited and simply identified? Perhaps the only method possible is to develop field screening methods which will identify those lines which have yield advantage in stress. Further detailed investigation of these varieties to identify the different mechanisms involved can improve parental choice in crossing programs.

In the case of drought stress, for this approach to work, one must be able to create reproduceable conditions of water availability which allow the genetic differences to be identified. An important aspect of this approach is the ability to function without the interference of rain within the crop's life. In many countries this requirement is only satisfied by the use of rainshelters. However, in the winter and summer in Central India the opportunity exists to grow a crop with low probabilities of rain and with irrigation management produce water stress at any time and of the intensities desired to allow effective selection.

As the timing and duration of stress can also be easily varied using this approach it is possible to create within controlled circumstances a large number of moisture permutations which can then be related on a probability basis to seasonal

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patterns of rainfall in a given region.

Applying this method to groundnuts, we have established a screening process which produces 24 combinations of droughts varying in times of occurrence and intensity. This should allow us to identify germplasm which has desireable characteristics and the G x E interactions that may occur from stress occurring at different stages of crop growth.

This process is suitable for identifying differences in homozygous lines; however it does not allow for the selection of plants which have merit within segregating material derived from a crossing program. It is apparent from our results that apparently uniform lines in non-stress conditions still may contain much variability when subjected to a drought screen. However, the line source screening process may be used to select water applications which cause the largest differences to emerge within the population and this treatment (reflected at one point within the line source) can then be created over a larger area of uniform irrigation to allow successful identification of those segregants which have advantage.

Certain lines have the ability to grow better than others in droughts. However, in groundnuts there is also a major nutrient stress which may be induced by the unavailability of water. The pods act as roots in the soil and are well capable of contributing to the plant water supply, a characteristic perhaps very significant in exploiting light showers. However, if the soil in the pod zone is dry the uptake of

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water and calcium by the pods is decreased or impossible. The plant then relies on water uptake from depth by the roots but since the pods are not transpiring there is little or no movement of water to the pods and their requirements of calcium are not satisfied. This shortage of calcium may cause seed abortion.

Our drought screening exercises so far have shown that substantial differences in seed abortion may occur under water stress. Some lines experience almost no seed abortion, in others the seed abortion is substantial or complete.

At present the physiological reasons for this are not clear and are the subject of a study at ICRISAT. For this reason drought resistance of the whole plant (that is the ability to continue accumulating dry matter during drought) needs to be combined genetically with those characteristics which prevent seed abortion.

Manipulation for improvement in stress environments often requires an acceptance of a loss in yield potential in good environments. The physiological reasons for this need further research, but the implications to the breeder are considerable and he should be prepared to approach the problem without preconceived ideas on the sources of material which may be useful to him.

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