19 A Physiological Approach to the Understanding of Genotype by Environment Interactions – A Case Study on Improvement of Drought Adaptation in Groundnut

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Abstract

Current phenotype models utilized by plant breeders partition traits, such as reproductive yield (Y), into the 'statistical' components of genetic (G), environmental (E), and genotype by environment (G×E) interaction. Traits such as yield commonly have large G×E interaction terms. Breeders often have little information concerning the physiological basis of this G×E interaction, thus leaving them without a clear idea of how to further exploit the material. Better knowledge of the physiological basis for the differential responses of genotypes to specific environments should improve the efficiency with which the breeder can characterize material for its G, and G×E interaction, and hence increase the speed at which superior genotypes can be identified.

This chapter describes a simple physiological model to improve the understanding of the basis of G×E interactions in groundnut under drought conditions.

The physiological model, proposed by Passioura was used to define the yield (Y) as the product T × TE × HI, where T = amount of water transpired, TE = transpiration efficiency and HI = harvest index. Past and current studies have attempted to quantify these components in easily measurable ways. TE in peanuts was measured via carbon isotope discrimination and specific leaf area. HI was estimated by measuring pod yield and total dry matter at maturity. T was estimated by substituting estimates of Y, TE, and HI in the identity above.

The model components were analysed from an experiment consisting of 50 genotypes grown across multiple environments (seven locations, three water treatments and three replications).

The results from this analysis enables us to:

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1. obtain additional information on G×E interactions with very little extra investment in time and resources, since the parameters of the model could be measured simply and economically,
2. facilitate selection of parents/genotypes with specific adaptive traits, and
3. highlight negative associations between yield determining traits.

The various assumptions in the proposed model are being verified in an on going international collaborative project involving Indian and Australian scientists.

Introduction

The existence of genotype by environment (G×E) interactions for grain yield in crops has complicated selection and breeding strategies for many years. G×E interaction is noticeable when genotypes being evaluated rank differently among trials conducted in different locations and seasons. In the past, considerable attention has been diverted to the development of statistical procedures to investigate this phenomenon in multi-locational data sets based mostly on observations of grain yield (Kang, 1990). A significant G×E interaction for a complex trait such as yield, reduces the usefulness of genotype means across environments for selecting superior genotypes. Thus, selection for yield in a sample of environments has been a largely empirical procedure, which is very slow and expensive per unit genetic gain.

Current phenotype models partition quantitative traits, such as yield (Y), into the 'statistical' components of genetic (G), environmental (E), G×E interaction, and error. Traits such as yield commonly have large G×E interaction terms. Breeders often have little information concerning the physiological basis of this G×E interaction, thus leaving them without a clear idea of how to further exploit the material. The role of physical environmental factors (Freeman and Perkins, 1971) and biotic factors (Gravois *et al.*, 1990) in explaining G×E interactions has received recent attention. A number of approaches have tried to link climatic components, such as temperature, solar radiation or a combination of various environmental factors, with yield. These attempts have had only limited success because climatic variables are confounded, and there is no mechanistic basis for studying the variation in crop performance.

An alternative approach is to quantify the effects of environmental factor(s) on different physiological processes contributing directly or indirectly to the yield variation, and incorporating these relationships into crop growth models (Muchow *et al.*, 1991; Carberry and Muchow, 1992) to assess genotypic performance across environments. Better knowledge of the physiological basis for the performance of genotypes in variable environments should improve the efficiency with which the breeder can characterize material for its G, and G×E interaction, and hence increase the speed at which superior genotypes can be identified/developed.

Simple analytical crop models, such as those proposed by Monteith (1977), Passioura (1977) and Duncan *et al.* (1978), provide a good framework for the understanding of yield variation among different genotypes in variable environments, provided the effects of environment on the physiological processes contributing to yield are quantified. At the present time, these models probably offer

the most scope for improving the efficiency of selection in breeding programs because, for a relatively minor investment in extra data collection, an improved physiological understanding of genotypic variation in yield performance under differing environmental conditions can be obtained.

This chapter gives a case study of how a simple physiological model might be applied in a practical breeding program. An overview of this approach, and a brief description of appropriate simple physiological models, has been given by Bidinger *et al.* (Chapter 17, this volume). The concept of how E and G×E interaction effects in multi-environment trials can be better understood and quantified via the use of these simple models, is further explored using a simple water resource model applied to groundnut.

Physiological Model

The model, originally proposed by Passioura (1977), states that pod yield (Y_p) under water limited conditions is given by the identity:

$$Y_p = T \times TE \times HI \qquad (19.1)$$

where, T is the amount of water transpired by the crop (in mm), TE is its efficiency of use in dry matter production (g dry matter per kg water transpired), and HI is the proportion of total biomass partitioned into pods, or the harvest index (HI). The three parameters of the model i.e. T, TE and HI and their product Y_p, are significantly influenced by the environment as well as the genotype. Analysis of Y_p within this framework provides a basis for understanding genotypic variation across a range of environments.

Current studies with groundnut (Wright and Nageswara Rao, 1994b) are attempting to measure/quantify the parameters of this model across a wide range of environments, so that their contribution to genotypic yield variation and to G×E interactions, can be better understood and the knowledge used to improve plant breeding practice.

For any model to be useful in improving the efficiency of a breeding program, it is essential that the parameters are easily and simply obtained, so that breeders can use and apply them without substantial investment in time and data collection. In general, crop physiologists have not appreciated this constraint faced by breeders, and have therefore not been able to adequately extend and/or apply their often very relevant findings to 'real life' breeding programs. Williams (1992) recently proposed how a simple analytical model approach, using the parameters of crop growth rate, partitioning and phenology, could be used for interpretation of data from multi-location groundnut trials. In this chapter we present an approach to measure/estimate the model parameters of equation (19.1), so that these technologies could potentially be applied in breeding programs.

Transpiration efficiency (TE)

Variation in TE can occur due to both environmental and genetic factors. The following expression for TE illustrates these sources of variation:

$$TE = A/g_s = (p_a(1 - p_i/p_a)/1.6\,(e_i - e_a) \quad (19.2)$$

where A is the assimilation rate (in μmol m^{-2} s^{-1}), g_s is the stomatal conductance (in mol m^{-2} s^{-1}, e_i and e_a (mbar), p_i and p_a (ppm) are the inter-cellular and atmospheric vapour pressures for water and CO_2, respectively.

From the genetic point of view, it can be seen from equation (19.2) that decreases in p_i/p_a at the leaf and canopy level will increase TE at a given $e_i - e_a$, or vapour pressure deficit (VPD) between the leaf and air. Significant genetic variation among groundnut genotypes in p_i/p_a, and hence TE, has been observed (Hubick *et al.*, 1986, 1988). The balance between A and g_s will ultimately determine the magnitude of p_i/p_a. In groundnut, it appears that increases in leaf assimilation rate (A) relative to g_s, which cause p_i to fall and TE to increase, are responsible for the observed genotypic variation (Hubick *et al.*, 1988; Wright *et al.*, 1988, 1994).

Equation (19.2) also indicates that TE can be strongly influenced by environmental changes in VPD between the air and leaf. For instance, growing crops in semi-arid conditions where VPD is high, will substantially reduce TE. Thus, the same genotype grown in environments with contrasting VPD will have substantially different TE values.

Tanner and Sinclair (1983) introduced a simple concept to enable comparison of TE among species and cultivars, independently of VPD. They stated that TE was inversely proportional to the average VPD, with k being the constant of proportionality, i.e.:

$$TE = k/(e_i - e_a). \quad (19.3)$$

Thus, using this simple analysis, it is possible to use k to compare TE, independently of VPD, and hence look for genotypic variation without confounding due to environmental effects.

Although large variation in TE has been recently observed in groundnut, it cannot be easily exploited due to practical difficulties associated with its measurement, particularly in the field situation, which requires accurate estimates of root biomass and transpiration. This limitation may have been overcome following recent research that has found significant correlations between TE and leaf carbon isotope discrimination (Δ) for groundnut under both glasshouse (Hubick *et al.*, 1986, 1988) and field (Wright *et al.*, 1988, 1994) conditions. Theory predicts that TE and Δ should be correlated at the leaf level in C3 plants, via independent links to p_i/p_a (see Farquhar *et al.*, 1982). The Δ measurement therefore provides an integrated measure of p_i, and hence TE, over the life of the plant. This research has therefore raised the possibility of using Δ as a rapid, non-destructive measure for selection of high TE in large-scale groundnut breeding programs.

Despite its close correlation with TE, Δ is still very expensive to analyse in plant tissues, costing around US$20 per sample. However, further research suggests there may be a cheaper surrogate measure available, with the finding that highly significant relationships between TE (and Δ) and specific leaf area (SLA, cm^2 g^{-1}) exist over a wide range of genotypes and environments (Nageswara Rao and Wright, 1994), thus opening up new possibilities for utilization of a rapid and economical screening tool to identify genotypes with high TE in large-scale breeding programs.

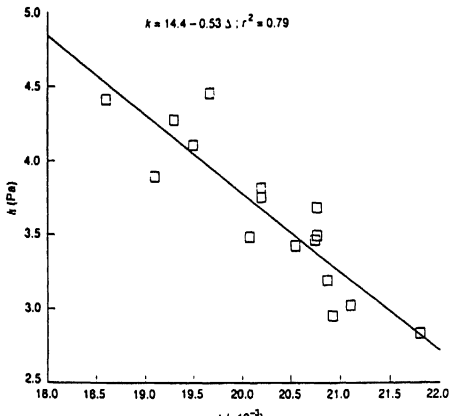

Fig. 19.1. Relationship between transpiration efficiency coefficient (k) and leaf carbon isotope discrimination (Δ) for data derived from groundnut transpiration efficiency studies in field based mini-lysimeters.

In order to allow comparisons of groundnut genotypic differences in TE (based on Δ or SLA) that are independent of VPD differences due to environment/location, Wright and Nageswara Rao (unpublished data) have further analysed the field data of Wright *et al.* (1988, 1994) to derive a relationship between Δ and k for groundnut. Values of k from a range of groundnut germplasm, which differed in TE under well-watered and water-stressed conditions (Wright *et al.*, 1988, 1994) were calculated from equation (19.3), and regressed against the measured Δ. Fig. 19.1 shows the significant linear relationship (r^2=0.80) found. This shows that estimates of VPD corrected TE could be obtained from Δ measurements. Wright and Nageswara Rao (unpublished data) have also used the theoretical approach described by Hubick and Farquhar (1989) to show that there is close agreement between theoretical and measured responses between k and Δ. Further detailed experiments to measure TE and Δ in contrasting VPD environments are needed to validate the generality of this relationship.

The situation with TE estimated from SLA is not as clear, as the mechanistic and theoretical basis of the relationship is not as yet understood. Highly significant linear relationships between Δ (and hence TE) and SLA have been observed for genotypes grown over a range of environments (Table 19.1). The slopes and intercepts of the regression equations (Table 19.1) are reasonably similar among

Table 19.1. Regression equations relating specific leaf area (SLA) to Δ for a range of peanut genotypes over contrasting environments.

Regression equation	r^2	Comments	Source
Δ = 15.0+0.038(SLA)	0.87	Kingaroy, Bundaberg (Australia) well watered, and drought stress 4 genotypes	Nageswara Rao and Wright (1994)
Δ = 14.2+0.04(SLA)	0.81	Kingaroy (Australia) drought 4 genotypes	Wright *et al.* (1994)
Δ = 16.4+0.033(SLA)	0.51	Kingaroy (Australia) well watered 300 F_3 lines	Wright *et al.* (1992)
Δ = 14.0+0.033(SLA)	0.91	Kingaroy, Bundaberg (Australia) cv. Tifton, different canopy positions	Wright and Nageswara Rao (1994b), Wright and Hammer (1994)
Δ = 13.4+0.039(SLA)	0.51	10 genotypes water deficit at ICRISAT, Hyderabad, India	Nageswara Rao *et al.* (1993)
Δ = 12.2+0.037(SLA)	0.53	6 genotypes irrigated and droughted, ICRISAT, Hyderabad,India	Nageswara Rao *et al.* (1995)

environments. The apparent stability of this relationship across genotypes and environments raises the possibility of deriving estimates of TE from SLA measurements, via a relevant Δ/SLA relationship (Table 19.1), by using equation (19.4) and an average VPD for a specific site. In practice, it will probably be necessary to derive the slope and *y* intercept for this relationship for a subset of genotypes in specific environments to ensure that reliable Δ estimates from SLA measurements are achieved. For the current example we use an averaged form of the relationships presented in Table 19.1, as:

$$\Delta = 0.03\ (SLA) + 14.0 \qquad (19.4)$$

In summary, we propose that it should be possible to derive estimates of VPD corrected TE for specific genotypes in given environments using equations 19.3 and 19.4, and Fig. 19.1, with measurements of Δ and/or SLA, and average VPD over a season.

Harvest index (HI)

HI can be easily estimated in conventional breeding programs by the additional measurement of total dry matter (TDM) at maturity. These estimates will be reliable when leaf material is retained until maturity, however there can be problems in groundnut where severe drought stress or foliar diseases cause leaves to abscise before maturity. Where foliar diseases are likely, it is suggested that adequate prophylactic chemical control is applied to ensure leaf material is retained, and hence an accurate estimate of TDM and HI are obtained. Where severe end-of-season drought causes premature senescence of all genotypes within a breeders population, Wallace *et al.* (1993) suggests that abscised leaves, and even remaining leaves on some genotypes, be ignored (and removed) to improve the uniformity of comparison

in HI across genotypes. Comparisons are probably still valid based on a stem only basis, and Wallace *et al.* (1993) even suggest that fresh weights of aerial organs may be adequate for some crops to facilitate rapid processing of multiple genotypes in a breeding population.

Transpiration (T)

The ability of certain genotypes to access and exploit soil water reserves deep in the profile can increase T and potentially Y_p. Significant genotypic variation in this character has been demonstrated in groundnut (Wright *et al.*, 1991), suggesting that selection could be possible in breeding programs. Unfortunately, T is currently much more difficult to measure/estimate than either TE or HI. While total evapotranspiration (ET) can be quantified using gravimetric techniques under both glasshouse and field conditions, and by other technologies such as neutron probe and Time Domain Reflectrometry (TDR) in the field, there are still many problems in accurately apportioning water loss due to crop water use (i.e. T) and soil evaporation (Turner, 1986). There are further practical problems in screening large numbers of genotypes in a breeding program using these techniques.

Another, as yet untested, method we plan to investigate is the estimation of T by 'reverse engineering' of the TDM component of equation (19.1). That is, given:

$$\text{TDM} = T \times \text{TE}. \tag{19.5}$$

Then T could be estimated by re-arranging equation (19.5) to:

$$T = \text{TDM}/\text{TE}. \tag{19.6}$$

There are, however, some assumptions and potential sources of error that need to be taken into account in this analysis. First, our estimate of TE from either Δ or SLA measurements would need to be corrected for the effect of the prevailing VPD. This should be possible using the approach described in the previous section on TE estimation. Second, our TDM measurement at maturity only accounts for above-ground DM, and thereby excludes root DM. In practical terms, it is of course very difficult to easily and accurately recover roots for numerous genotypes from field plots. This under-estimation of TDM will therefore lead to errors in the final T derived from equation (19.6). The errors may, however, be within acceptable limits based on our current knowledge of root and shoot relationships. For instance in groundnut, it appears that roots account for only a small percentage (1–2%) of the TDM by maturity (McCloud, 1974; Enyi, 1977), although it needs to be kept in mind that the proportion of root dry matter can increase substantially under conditions of water stress. In addition, a strong correlation between root dry weight and shoot dry weight exists in groundnut, under both glasshouse (Ketring, 1984; Pandey and Pendleton, 1986) and field conditions (Wright and Nageswara Rao, 1994a). Thus, it is likely that errors for genotypic comparisons of T (derived from equation (19.6)) will be minimal. The reverse engineering model now needs to be verified further with field measurements of T and root DM.

A Case Study in Groundnut – Preliminary Findings

An international collaborative project, involving the Australian Centre for International Agricultural Research (ACIAR), the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), the Indian Council for Agricultural Research (ICAR), the Queensland Department for Primary Industries (QDPI) and the Australian National University (ANU), entitled 'Selection for Water-Use Efficiency in Food Legumes', began in July 1993. One of the aims of the project was to investigate the approach set out above for groundnut. This has proceeded by conducting experiments incorporating a large number of genotypes with varying TE and HI characteristics in a wide range of environments throughout India (see Wright and Nageswara Rao, 1994b for further details). In these trials, detailed growth analysis and SLA measurements on up to 50 genotypes over three contrasting watering regimes, plus extensive climate data collection are being conducted. The data will allow quantification of the G×E interactions for pod yield and its physiological components (T, TE and HI) using the approach set out above. Information on the relative magnitudes of G×E interaction for yield and its components will therefore be possible.

One season of experiments has been fully completed, and data have been gathered and some preliminary data analysis made. We present some preliminary findings from these multi-location trials to demonstrate how the simple physiological model can be used, and discuss how a more detailed understanding of the G×E interaction might be utilized.

Two separate experiments were conducted at each site. The first involved 50 groundnut genotypes grown under fully irrigated or rainfed conditions (Expt 1). The second experiment (Expt 2) involved a subset of 20 genotypes grown under three watering regimes, namely, fully irrigated, rainfed and a mid-season stress applied using rain-out shelters located at each site. The genotypes used had approximately similar duration. Trials in years two and three of the project will assess yield performance, and its physiological components, over a much more diverse range of germplasm.

Table 19.2. Summary of weather at seven experimental sites in India during rainy season 1993.

Location	Total rainfall (mm)	Mean temp Max. (°C)	Mean temp Min. (°C)	Mean evap. (mm)	Mean SVPD* (MPa)	Drought phase
Vridhachalam	681	33	–	2.9	–	–
Tirupati	821	32	23	4.7	1.34	Nil
UAS	837	27	19	4.8	1.01	Nil
IAC	560	31	22	5.7	1.22	Flowering
Jalgaon	619	32	21	3.7	1.68	Nil
Junagadh	361	33	24	-	1.43	Podfill
Durgapura	414	33	21	5.7	1.77	Podfill

* Soil vapour pressure deficit.

Table 19.3. Summary of crop growth parameters for 50 genotypes grown under irrigated (IRR) and rainfed (RF) conditions during 1993 rainy season at seven centres in India.

Centre	Treatment	T (mm)	TE (g kg^{-1})	HI	Y_p (g m^{-2})	$TBIO_{adj}$ (g m^{-2})
Vriddhachalam	IRR	90	3.02	0.30	47	269
	RF	103	3.20	0.31	60	330
Tirupati	IRR	457	3.21	0.52	456	1463
	RF	368	3.35	0.50	372	1230
Bangalore	IRR	316	4.06	0.50	390	1270
	RF	285	4.12	0.53	373	1158
IAC	IRR	217	3.59	0.41	195	779
	RF	214	3.63	0 38	228	777
Jalgaon	IRR	589	2.57	0.38	341	1489
	RF	524	2.68	0.38	316	1370
Junagadh	IRR	173	2.98	0.25	75	518
	RF	63	3.13	0.05	6	198
Durgapura	IRR	354	2.67	0.48	272	943
	RF	193	2.82	0.27	87	542
Mean	IRR	314	3.16	0.40	254	962
	RF	250	3.27	0.36	206	800
SE±		38.8	0.13	0.04	30.8	97.7
CV(%)		23.2	6.9	17.0	22.9	18.9

The climatic conditions experienced during the season varied substantially from site to site, (Table 19.2), and in general, drier conditions prevailed in the northern compared with the southern sites. Pod yields (Yp) and total biomass ($TBIO_{adj}$) varied substantially over sites and irrigation treatments. Total biomass was the amount after adjusting for higher energy content of pods (Duncan *et al.*, 1978). Tables 19.3 and 19.4 show the mean genotypic response at each site and irrigation treatment for Expts 1 and 2. Yield levels were very low at the Junagadh (Jung) and Vriddhachalam (Vrid) sites, even under fully irrigated conditions. Poor plant stands at Vrid were largely responsible for this effect, while very high temperatures and VPD during the growing season at Jung were thought to severely limit yields. Another possible cause was due to severe aphid infestation in the early stages of growth. Analysis of variance over multi-location sites showed highly significant effects for G and GxE interaction (location and irrigation regime) for both Y_p and $TBIO_{adj}$ (data not shown).

The simple modelling approach, as outlined above, was applied to the data collected from Expt 2, where 20 genotypes were grown over seven sites and under three varying water regimes (i.e. 21 different environments). Estimates of TE were calculated from equations (19.3) and (19.4) using SLA measurements for each genotype, and mean VPD measured over the season at each site. T was estimated from equation (19.6), using $TBIO_{adj}$ measurements and TE estimates. Harvest index (HI) was calculated as the ratio of pod dry matter to TDM at maturity. Means over genotypes for each parameter estimate for experiments 1 and 2 are presented in Tables 19.3 and 19.4. We stress here that there are many assumptions used in calculating these parameter estimates (outlined in Section 2), however, they should give

Table 19.4. Summary of crop growth parameters for 20 genotypes grown under irrigated (IRR), simulated drought (ROS), and rainfed (RF) conditions, during 1993 rainy season at seven centres in India.

Centre	Treatment	T	TE	HI	Y_p	$TBIO_{adj}$
Vrid	IRR	91	3.1	0.30	48	277
	ROS	81	3.5	0.29	47	280
	RF	101	3.2	0.30	57	324
Tirupati	IRR	443	3.2	0.52	451	1425
	ROS	422	3.3	0.52	434	1398
	RF	365	3.4	0.51	374	1229
Bangalore	IRR	332	4.2	0.53	447	1376
	ROS	206	4.2	0.65	340	862
	RF	308	4.1	0.54	412	1249
IAC	IRR	220	3.6	0.69	337	792
	ROS	274	3.6	0.73	435	978
	RF	224	3.6	0.81	408	817
Jalgaon	IRR	621	2.5	0.37	337	1528
	ROS	535	2.7	0.35	293	1432
	RF	529	2.7	0.38	317	1410
Junagad	IRR	175	3.1	0.24	72	538
	ROS	178	3.1	0.22	66	547
	RF	67	3.2	0.10	8	214
Durgapura	IRR	369	2.7	0.48	288	990
	ROS	282	2.6	0.43	183	717
	RF	193	2.8	0.28	90	542
Mean	IRR	321	3.2	0.45	283	989
	ROS	283	3.3	0.46	257	888
	RF	255	3.3	0.41	238	825
SE±		40.5	0 13	0.044	35.07	103.02
CV(%)		24.2	6.7	17.1	23.1	19.3

us a reasonable indication of the relative genotype performance across a range of contrasting environments.

To illustrate how these model parameters might improve a breeders understanding of G×E interactions for pod yield, we used a standard stability analysis (Finlay and Wilkinson, 1963), which was applied to the yield data and to the physiological determinants of yield, derived from the simple model. Results of this analysis are presented for a group of four contrasting genotypes (ICG 1697, Fig. 19.2a, ICG 476, Fig. 19.2b; TMV2 NLM, Fig. 19.2c; ICGV 86031, Fig. 19.2d), with some points of interest noted for each:

1. ICG 1697 – Pod yield response indicated this genotype was below average under environments with low water availability, and above average under better water status. Interestingly, this response was closely associated with the HI response across environments, while T was above average and TE followed the average genotype trend across environments. It could be suggested that partitioning of carbon to pods in this genotype may be particularly affected under conditions of

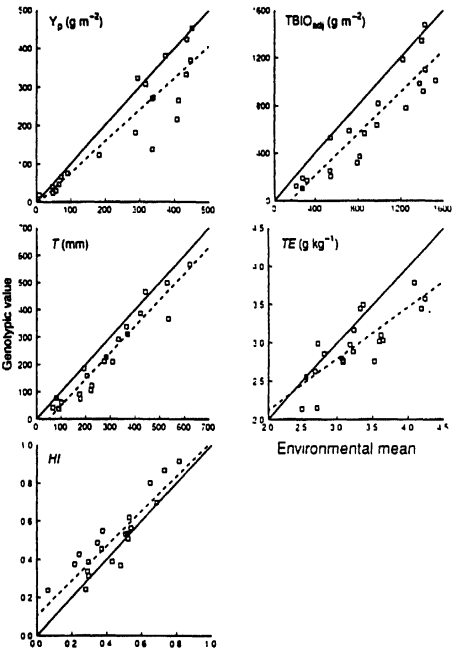

Fig. 19.2a

Fig. 19.2. Stability of pod yield, transpired water, transpiration efficiency and harvest index for four genotypes ((a) – ICG 476; (b) – TMV2 NLM; (c) – ICG 1697; (d) – ICGV 86031) exposed to environments with varied water supply and climatic conditions.

limited carbon supply arising from water deficits, as was hypothesized by Bidinger *et al.* (Chapter 17, this volume).

2. ICG 476 – Pod yields over the entire range of environments were well below the mean genotype response (20 genotypes). Below average T and TE across the range of environments were largely responsible. However, very high HI levels, particularly at environments with low water availability, compensated for these low T and TE levels.

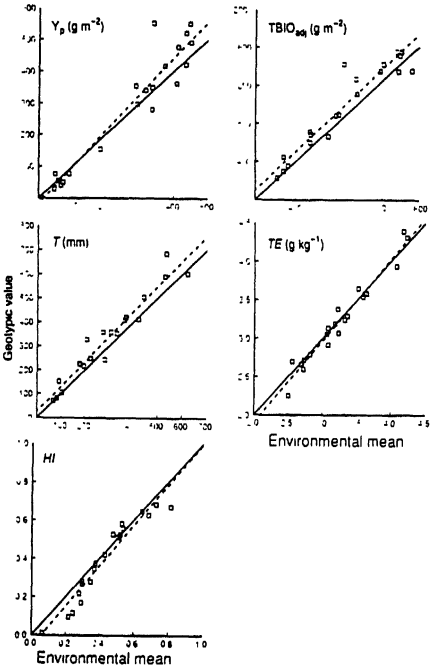

Fig. 19.2b

3. TMV2 NLM – This genotype is a narrow leaf mutant (NLM) of the widely grown and well-adapted TMV-2 variety. The pod yield response indicates that while average yields occurred in water deficit environments, in environments with better water availability, yields declined dramatically. Although TE remained well above the genotype average in most environments, T and HI were well below average, particularly under conditions of higher water availability.
4. ICGV 86031 – While pod yield of this genotype was close to the mean response under water deficit conditions, and lower than the mean under non-limiting

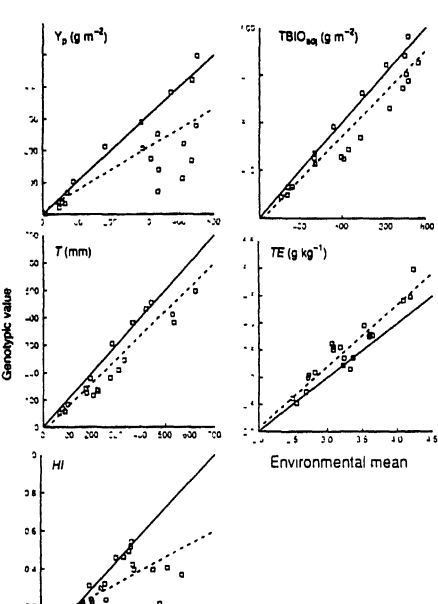

Fig. 19.2a

environments, the genotype had above average TE across a range of environments, however T and HI were lower in environments with better water availability.

This simple physiological analysis of genotypic pod yield variation in response to changing environment (i.e. water availability) illustrates how the different determinants of yield (i.e. T, TE, HI) can differentially interact to determine ultimate yield. In particular, the above examples show that while a particular genotype may have, for instance, high TE over a wide range of contrasting water environments, the other determinants may be expressed at below average levels. This effect is well

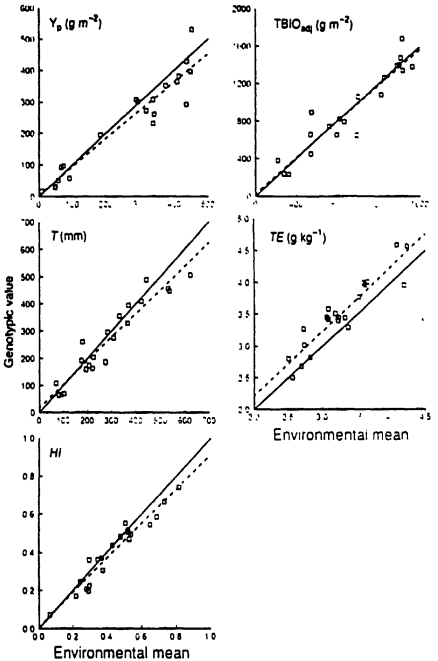

Fig. 19.2d

illustrated in our last three genotypes noted above, where TE and Y_p appear to be negatively associated. This negative association has been observed previously (Wright *et al.*, 1988; Hubick *et al.*, 1988; Wright *et al.*, 1992), and could arise due to either a genetic or physiological linkage. Further research in this project plans to investigate the extent and nature of this association.

The ultimate aim of groundnut breeding programs is to identify/develop genotypes with high pod yield across a wide range of environments. The above analysis has indicated that significant G×E interaction for, as well as negative associations

among, the yield determining traits, occurs widely in groundnut. It would appear that these effects may be largely responsible for the slow rate of progression of yield enhancement in breeding programs. For example, it is possible that breeders may be culling out potentially useful genotypes with high total biomass production (i.e. high T and/or TE), because they may have extremely low HI. It should be possible to combine high HI characteristics into these genotypes, thereby improving overall pod yields. The approach outlined here should enable a more thorough understanding of the potential occurrence of these interactions in variable environments, thus allowing the selection of genotypes with high levels of each trait to improve adaptation of genotypes in a given environment. For example, genotypes with high T and/or TE could be selected in environments favouring the expression of these traits.

There is a clear need to now combine the advances in physiological understanding of G×E interactions, as outlined here, with current advances in analysis of G×E interactions by statistical methods (as outlined in Section II of this book). The challenge remains for breeders, physiologists and modellers to 'start talking the same language' so that this combined approach can succeed. Until recently, scientists in respective disciplines have tended to work in isolation, largely because of a lack of in-depth knowledge in their counterparts' fields. What is now required is the setting up of dedicated teams of scientists with common goals, philosophies and research objectives. The effective combining of traditional and physiological approaches to crop improvement will not happen until this collaboration has been achieved.

Conclusions

Breeders often have little information concerning the physiological basis of G×E interactions for pod yields, thus leaving them without a clear idea of how to further exploit genetic material. Statistical methods of analysis have been employed to solve this problem, however this process can be very slow and costly per unit of genetic gain. Crop physiological models can be used to improve the breeders understanding of the physiological reasons behind G×E interactions, and hence may greatly improve the efficiency of current selection practices.

A number of simple crop physiological models which involve a few mechanistically based parameters are currently available. The parameters required in these models need to be easily, accurately and economically measured before breeders can effectively utilize them in large-scale breeding programs. There is a clear need for developing simple methods of measurement for these parameters. There will be a need for breeders, physiologists and crop modellers to collaborate more extensively in the development of appropriate traits for selection, their simple measurement, and refined methods of data analysis so that superior genotypes can be selected more quickly and efficiently.

A case study using the water resource model in groundnut breeding programs is described here. Simple technologies are described to estimate or infer the parameters of water transpired, transpiration efficiency and partitioning of dry matter to pods. The preliminary analysis of a multi-location data set involving 20 genotypes

over 21 differing environments illustrates how a detailed understanding of the physiological reasons behind GxE interactions can be achieved for little extra investment in time and data collection The analysis highlights how more rapid pathways to yield improvement might be found and the need for breeders to be aware of negative associations between yield determining factors There will be a need for concurrent selection of all traits to ensure negative associations are not introduced into the selection procedure

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