Heritability of Drought–Resistance Traits in Peanut

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Abstract

The paper presents results from a case study on genetic enhancement of drought resistance in peanut using combined physiological and breeding methods. Peanut genotypes with high levels of components of a resource capture model, transpiration (T), transpiration efficiency (TE) and harvest index (HI), were used as parents in a hybridisation program. F_2-derived families of peanuts from 4 crosses were subjected to trait-based among family index selection in the F_3 and F_4. In order to calculate the selection index, estimates of harvest index, transpiration efficiency and transpiration were obtained. Heritability estimates for these traits were estimated using 3 different bases i.e. broad-sense heritability on an F_3 row basis, broad-sense heritability on an F_4 family mean basis using variance components and standard unit heritability estimates using correlation among generations.

The heritability estimates varied significantly between crosses and traits depending on levels of genetic variation in parents. In some cases the variation seems to be caused by errors in sampling method.

Kernel yield (KY) generally had the best correlations between F_3 and F_4 (maximum 0.65), HI and TE were intermediate and correlations for T were very poor (one cross in one environment 0.56 the remainder not significant).

Consideration of these differences in heritability and the costs of sampling lead to the proposal that a simpler index based on KY and TE may be a useful compromise for selection of superior drought performance in peanut. Use of an index including TE would prevent selection for decreasing TE when selecting for KY, where there are casual negative associations between TE and the other two components.

Media summary

It is possible to breed peanut varieties that produce more yield from the same amount of rainfall by selecting for a combination of high transpiration efficiency and kernel yield.

Key Words

Drought tolerance, peanut, breeding, transpiration efficiency, kernel yield.

Introduction

The yield of peanut in India and Australia is usually severely limited by water deficits during crop growth, arising from unpredictable rainfall, high evaporative demands and production on low water holding capacity soils. The breeding of more drought resistant genotypes is a strategy to increase productivity in drought prone environments. New breeding approaches utilising physiological traits have been proposed to improve the efficiency of selection for superior drought tolerant genotypes. Most of these efforts to date have however been unsuccessful, as the specified traits have been considered in isolation and have not necessarily been related to superior performance under drought stress.

New opportunities to develop higher yielding drought tolerant peanut genotypes emerged in the ACIAR-DPI project – ‘Selection for WUE in Food Legumes’, which developed a detailed understanding of the physiological factors determining yield in water-limited environments (Wright et al 1996). A resource capture model proposed by Passioura (1977) was used to analyse pod yield variation under water limited conditions in terms of three functional components i.e transpiration (T), transpiration efficiency (TE) and harvest index (HI). If these traits have significantly greater heritability than yield, or if they can be measured at lower cost, they will provide an avenue for more effective selection for yield under water-limited conditions. A subsequent project applied a trait-based selection strategy in 5 breeding programs (4 in India, 1 in Australia) (Rachaputi et al 2000). This paper presents results of different estimates of some genetic parameters for the water-capture-model traits from the F_3 and F_4 generations in the Australian breeding program.

Methods

Genetic material

Genotypes with high levels of T, TE and HI were selected from a wide range of germplasm screened in the ACIAR-funded project conducted in India and Australia (Wright and Nageswara Rao 1994). A selection of these genotypes were intercrossed to provide populations for selection studies. The four Australian crosses are presented in Table 1.

Table 1. Crosses used in the selection studies.

Cross code	Female parent	Traits	Male parent	Traits
AX1	Streeton	High T, medium HI, low TE	CSMG 84-1	High T, medium TE, low HI
AX2	ICGV 86031	High TE, low T & HI	TAG 24	High HI, medium TE, low T
AX3	TAG 24	High HI, medium TE, low T	CSMG 84-1	High T, medium TE, low HI
AX4	Streeton	High T & HI, low TE	ICGV 86031	High TE, low T & HI

Experimental design and traits measured

Up to 500 F_3 rows (from unselected F_2 plants) per cross were grown under non-limiting water conditions. All the selection was conducted at 90 cm row spacing. All were assessed for kernel yield (KY), total shoot dry matter (TDM), TE (via SPAD – a measure of chlorophyll content), HI and T estimated using the methods of Wright et al. 1996. TDM was estimated from 0.9 m^2 quadrats at maturity, KY was estimated from the remainder of the plot. HI was calculated from the independent estimates of TDM and KY to avoid manual separation of pods and vegetative material. SPAD readings were measured twice during the crop growth cycle, the single reading with the greatest precision was used to estimate TE (Nageswara Rao et al. 2001). A value was calculated for each progeny using a selection index (*S*) derived from the traits T, TE and HI (Chandra et al 2003). The top 50 F_2-derived families of were carried forward to the $F_{2:4}$ generation.

The $F_{2:4}$ families were divided equally between irrigated and rainfed experiments, and the same measurements made as in the F_3 generation. For selection in the F_3 there was one experiment per cross, with F_3 rows unreplicated with replicated check plots of the commercial variety Streeton. In the F_4, 50 families per cross were divided into 25 each for an irrigated and a rainfed experiment. Each of the eight F_4 experiments was a 3 replicate, 30 entry lattice with 5 check varieties.

Selection procedure

The three traits (T, HI and TE) were combined into the following selection index:-

$S=\sum_j (x_j-med_j)/QR_j,\ QR_j=\{Q_{3(j)}-Q_{1(j)}\}$

Where, x is…. Q_1 and Q_3 are the first and third quartiles, and in our case there are j = 3 traits (T, HI and TE) included in the index, a modification of index S7 of Chandra et al (2003). The index, *S*, ensured that selection was not influenced by extreme values and gave equal weighting to each trait. Median and quartiles were used so that no assumptions were made about distribution(s) of the data.

Estimates of heritability

Following Nyquist (1991) broad-sense heritability was estimated in the F_3 by using the variation of Streeton plots within each experiment as an estimate of environmental variance, and in the F_4 restricted maximum likelihood (REML) variance components were used to calculate broad-sense heritability on a progeny mean basis. Standard unit heritabilities (Frey and Horner 1957) or intergeneration correlations were calculated by the Pearson's correlation between F_3 and F_4. These three estimates of heritability are not directly comparable as they each have a different basis, but comparisons among crosses are valid using the same basis.

Results and Discussion

Broad-sense heritability (H) estimates for KY varied from 17 to 78 % in the F_3 and 37 to 91 % in the F_4 (Table 2). Cross AX4 had higher H values in the F_4 but the correlation between generations was not significant. Crosses AX2 and AX3 had higher H in the F_4 with significantly positive correlation with the F_3. While there was some consistency between the F_4 H values and the correlations, neither aligned well with the estimates from the F_3 The F_3's are unselected populations so the potential genetic variability in each population is not truncated but the lack of replication reduces the precision with which the variation is measured. Conversely in the F_4, the replicated measurement ensured nearly all cross-environment combinations had a significant H of 70% or greater. Hence, for KY the F_3 estimates may indicate the presence of genetic variability however they are not good predictors of the effectiveness of selection as measured by the correlations.

Table 2. Estimates and indicators of kernel yield heritability.

	Broad-sense heritabilities (%)			F_3-F_4 Intergeneration Correlations ^{B}	
Cross	F_3	F_4 Irrigated ^{A}	F_4 Rainfed ^{A}	Irrigated	Rainfed
AX1	78	ns	49	ns	0.60
AX2	17	87	79	0.65	0.42
AX3	63	91	88	0.57	0.38
AX4	47	71	69	ns	ns

[A] ns = no significant progeny effect (P≤0.05). [B] ns = not significantly different from 0 (P≤0.05).

HI showed some similarities to KY with a wide range of estimates of H from the F_3. Cross AX4 had the lowest values of H and crosses AX2 and AX3 were more consistent in the F_4 over the two watering environments (Table 3). Despite similarities, generally the heritability of HI was poorer than that of KY particularly for the correlation between F_3 and F_4. One of the reasons for using physiological traits in selection is that they may have better heritability than direct yield measurement. The intergeneration correlation suggests this was not the case for HI with this genetic material.

Table 3. Estimates and indicators of Harvest Index heritability.

	Broad-sense heritabilities (%)			F_3-F_4 Intergeneration Correlations [B]	
Cross	F_3	F_4 Irrigated [A]	F_4 Rainfed [A]	Irrigated	Rainfed
AX1	55	ns	61	ns	0.42
AX2	62	75	59	0.44	ns
AX3	62	80	85	0.56	0.42
AX4	16	ns	58	ns	ns

[A] ns = no significant progeny effect (P≤0.05). [B] ns = not significantly different from 0 (P≤0.05).

All four populations showed moderate to high H for TE in the F_3 (Table 4). Only the AX4 cross had significant heritability for TE on all bases, possibly because it had the greatest contrast between the parental genotypes for this trait (Table 1). Eventual multi-site evaluation of these families (Cruickshank et al 2003) has shown that TE is the most stable model factor over sites and that the trait-based selection index was successful at improving TE but not the other physiological traits.

Table 4. Estimates and indicators of Transpiration Efficiency heritability.

	Broad-sense heritabilities (%)			F_3-F_4 Intergeneration Correlations [B]	
Cross	F_3	F_4 Irrigated [A]	F_4 Rainfed [A]	Irrigated	Rainfed
AX1	50	86	49	ns	ns
AX2	53	ns	ns	0.55	ns
AX3	71	ns	ns	0.46	ns
AX4	61	77	67	0.53	0.38

[A] ns = no significant progeny effect (P≤0.05). [B] ns = not significantly different from 0 (P≤0.05).

Heritabilities of T were generally poor (Table 5). This is not surprising as it is a second-order, derived estimate of T (i.e. T = TDM/TE). Also the 0.9 m^2 quadrat for estimation of TDM could be a probable source of experimental error. Washing and drying of the TDM sample incurs a substantial cost. Doubling the size of the sample may have helped the accuracy of the T estimate; it would drastically increase the total cost associated with this selection protocol.

Table 5. Estimates and indicators of Estimated Transpiration heritability.

	Broad-sense heritabilities (%)			F_3-F_4 Intergeneration Correlations [B]	
Cross	F_3	F_4 Irrigated [A]	F_4 Rainfed [A]	Irrigated	Rainfed
AX1	12	ns	ns	ns	ns
AX2	<0.001	53	46	ns	ns
AX3	54	ns	44	ns	0.56
AX4	70	49	ns	ns	ns

[A] ns = no significant progeny effect (P≤0.05). [B] ns = not significantly different from 0 (P≤0.05).

The smaller plant stature of TAG 24 and ICGV 86031 is much better suited to narrower row spacing and higher plant density. The lower T achieved under the wide row planting arrangement may have imposed a “maximum yield ceiling” on all progeny in cross AX2, and many progeny in AX3 and AX4, and reduced genetic variability (hence heritability) of T and KY in those 3 crosses. Cruickshank et al (2003) concluded that the choice of parents for those three crosses was not the most suitable for the Australian cropping system. Cross AX1 expressed only small variation in T but as the mean value for T was high (data not shown), low heritability for T in this cross points to potential fixation of desirable genes for high T.

This study demonstrated that it was possible to select and breed for higher TE using novel and cost effective selection tools such as SPAD chlorophyll meter readings (Wright et al., 1996). The SPAD meter provides a practical tool for breeding programs to now make improvements in TE and potentially T. Results from our studies clearly demonstrated that trait-based selection for high TE (via SPAD) was more efficient than empirical yield selection for improvement in TE (Cruickshank et al 2003). The challenge remains to be able to concurrently select for high levels of the three traits (T, TE, HI). TE and direct measurement of kernel yield had the most consistent intergenerational correlations while HI and T were less consistent. Heritabilities of T and HI are both dependent on the precision of TDM measurement, which cannot be improved without substantially increasing costs associated with sampling.

Conclusion

Kernel yield (KY) generally had significant correlations between F_3 and F_4, HI and TE were intermediate and correlations for T were very poor. This may be primarily due to the measurement of KY, which incorporates most of the plot, whereas HI and T estimation was dependent on a relatively small quadrat sample for shoot dry matter (TDM). Consideration of these differences in heritability and the costs associated with TDM sampling lead to the proposal that a simpler index based on KY and TE may be a useful compromise. KY integrates the effects of HI and T. Use of an index including TE will prevent selection for KY decreasing TE where there are casual negative associations between TE and the other two components.

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