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Prediction and Validation of the Frequency of Transgressive Recombinant Inbred Lines in Dolichos Bean (*Lablab purpureus* L. Sweet)

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Abstract

The use of an objective criterion to identify a few promising segregating populations from among a large number of such populations to select transgressive recombinant inbred lines (RILs) for use as pure-line cultivars would help enhance efficiency of breeding self-pollinated crops including dolichos bean. Allocation of resources only to a few such promising segregating populations is therefore assumes importance. The prediction of frequency of transgressive RILs that could be derived from advanced generations of segregating populations of crosses is one such criterion. We predicted the frequency of RILs that transgressed the better parent (HA 5) from segregating population derived from two elite but genetically diverse parents (HA 4 and HA 5) for primary branches plant^{-1}, pods plant^{-1}, pod weight plant^{-1} and grain weight plant^{-1} based on predictors such as mid parental value [m], additive genetic effects [a] and additive genetic variance [σ^2_A]. The predictors [m], [a] and [σ^2_A] were estimated using trait means of parents and their F_2 and $F_{2:3}$ generations based on both least square and mixed model methods. The predicted frequency of RILs was validated in F_4 generation. The frequency of transgressive RILs predicted using the predictors estimated based on least-squares as well as mixed-model was higher for primary branches plant^{-1} and grain yield plant^{-1} than for other two traits. However, the frequencies of transgressive RILs predicted using the predictors estimated based on mixed model was slightly higher than those predicted using the predictors estimated based on traditional least square method for all the traits except primary branches plant^{-1}. A fairly good agreement between predicted and realized frequencies of transgressive RILs for all the traits suggested reliability of the approach to predict the frequency of transgressive RILs. Implications of these results are discussed in relation to strategies to enhance the efficiency of breeding dolichos bean.

Keywords : Additive genetic effects, Additive genetic variance, Prediction, Transgressive segregation, Validation

Pure-lines are predominant cultivar types used for commercial production in self-pollinated legume crops including dolichos bean. Pedigree selection of desirable recombinant inbred lines (RILs) for use as pure-line cultivars from bi-parental crosses-derived segregating populations is the most widely used breeding method in dolichos bean (Ramesh and Byregowda, 2016). The breeders routinely develop a large number of bi-parental crosses-derived segregating populations to identify superior RILs through pedigree selection. Handling of a large number of segregating populations is prohibitively resource demanding. Even if it were feasible to handle a large number of segregating populations, it is unlikely to be efficient (Witcombe and Virk, 2001; Witcombe *et al.*, 2013 and Zhong & Jannink, 2007). The breeding potential of segregating populations depends on the performance of their best progenies (transgressive RILs) rather than the mean performance of all possible RILs derivable from them.

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A sizable number of crosses made between parental combinations that fail to produce transgressive RILs for use as cultivars consume over 99 per cent of the resources (Witcombe *et al.,* 2013). Allocation of resources only to large-sized segregating populations derived from a few promising crosses selected based on an objective criterion is expected to enhance the chance of identifying transgressive RILs for use as pure-line cultivars and thus help enhance breeding efficiency (Chahota *et al.,* 2007; Kuczynska *et al.,* 2007; Witcombe *et al.,* 2013; Bernardo, 2020 and Mezzomo *et al.,* 2021). Prediction of frequency of transgressive RILs that could be derived from advanced generations of segregating populations is one such criterion. Jinks and Perkins (1972) conceptualized the theory and out-lined the analytical procedure to predict the frequency of RILs that transgress pre-determined standards. The quantitative genetic parameters such as additive gene effect [a], mid parent value [m] and additive genetic variance [σ^2_A] reliably estimable from parental and early segregating generations (such as F_2 and F_3) are sufficient to predict the frequency of transgressive RILs (Jinks and Pooni, 1976). Jinks & Pooni (1980) and Thomas (1987) have demonstrated that even random sample of a few F_3 families provide a reliable estimate of [a] and [σ^2_A].The objective of the present study is to predict and validate the frequency of transgressive RILs from a cross derived from two elite parents in dolichos bean.

Material and Methods

The basic material consisted of two elite parents, namely HA 4 and HA 5 (Table 1). Both HA 4 and HA 5 are high yielding pure-lines cultivars released for commercial production of dolichos bean in eastern dry zone of Karnataka, India. While HA 4 produce relatively fewer branches, racemes and large-sizedcurved pods bearing large-sized grains, HA 5 produce relatively many branches, racemes and small-sized pods bearing small-sized grains (Table 1). The objective was to develop a new pure-line that producesa large number of branches, racemes and bigger-sized pods and grains. HA 4 × HA 5 cross was synthesized during 2020 rainy season at the experimental plots of the Department of Genetics and Plant Breeding (GPB), University of Agricultural Sciences (UAS), Bangalore, India. A total of 20 and 15 well-filled F_1 seeds could be obtained from HA 4 × HA 5 cross. The F_1 seeds were planted in 2020 post rainy season. All the F_1 seeds germinated and survived to maturity. The F_1 plants of the cross was carefully inspected for the traits specific to male parents to confirm their true hybridity. Indeterminate growth habit of all the 20 candidate F_1 plants confirmed the true hybridity HA 4 × HA 5 cross considering that indeterminacy is dominant over determinacy (Keerthi *et al.,* 2014; Keerthi *et al.,* 2016; Modha *et al.,* 2019 and Basanagouda *et al.,* 2022). The selfed pods from F_1's was harvested, hand-threshed and sun-dried to obtain F_2 seeds. F_2 plants were raised in 2021summer season. A spacing of 0.3m was maintained between F_2 plants. A total of 259 F_2 plants survived to maturity. Selfed pods from each F_2 plants were manually harvested, hand-threshed and seeds were sun-dried for use in raising $F_{2:3}$ populations during 2021 rainy season. The seeds of the two parents and randomly selected 144 $F_{2:3}$ families were planted in a single row of 3m length in randomized complete block design using two replications during 2021 rainy season. Fifteen-days after planting, seedlings of two parentsand 144 $F_{2:3}$ families were thinned to maintain a spacing of 0.3m between the plants and 0.6m between the rows. The recommended production

Table 1

Growth habit, photoperiod sensitivity and pedigree/source of parents used to derive crosses in dolichos bean

Parents	Growth habit	Responses to photoperiod	Pedigree/ Source	Reference
HA 4	Determinate	Insensitive	HA3 × Magadi local	Mahadevu and Byregowda (2005)
HA 5	Indeterminate	Insensitive	HA4 × GL153	Ramesh *et al.* (2018)

package was practiced to raise two parents, F_1, F_2 and $F_{2:3}$ generations. A total 12 plants in each of the four parents and within each $F_{2:3}$ families survived to maturity.

Sampling of Plants and Data Recording

Data were recorded on 10 randomly selected plants (avoiding border ones) from two parents, their F_1's and from each of the 144 $F_{2:3}$ progenies in each of the two replications and all the 259 individual F_2 plants for four traits, namely, number of primary branches and pods and weights of sun-dried pods and grains. The average of these traits across ten sample plants in each replication was computed and expressed as primary branches plant^{-1}, pods plant^{-1}, pod weight plant^{-1} (g) and grain weight plant^{-1} (g).

Estimation of Quantitative Genetic Parameters

Data recorded on 10 randomly selected individual plants in parents, their two reciprocal F_1's and 259 F_2 plants and replication-wise mean data of 10 randomly selected plants from each of the 144 $F_{2:3}$ progenies were used for estimation of thee quantitative genetic parameters, namely mid-parental value [m], additive gene effect [a] and additive genetic variance [σ^2_A] for use in prediction of the frequency of transgressive RILs that could be derived from HA 4 × HA 5 cross. Assuming additive-dominance (A-D) model, the parameters [m] and [a] were estimated using the multiple regression (Kearsey and Pooni, 1996) implemented in SPSS software version 16.0. Adequacy of A-D model was examined by joint scaling test (Kearsey and Pooni, 1996) implemented in SPSS software version 16.0. The [σ^2_A] was estimated by equating observed and expected mean squares (MS) due to 'between $F_{2:3}$ families' from analysis of variance (ANOVA) of $F_{2:3}$families and solving for σ^2_Aas $\sigma^2_A = 2 \times$ [(MS due to 'between $F_{2:3}$ families' - MS due to error) / number of replications] (van Ooijen, 1989). This analysis was implemented using statistical analysis option available in Microsoft Excel software.

ANOVA-based estimates of variance components are generally biased and can be negative, even though variances by definition must be either zero or positive. Restricted Maximum Likelihood (ReML) method which is based on linear mixed effects model is considered as the best alternative to least square method-based ANOVA for the estimation of components of variance (Patterson and Thompson, 1971). The REML method-based variance components always fall within the parametric space and are unbiased unlike those estimated using least-square method (Resende and Alves, 2020). Hence, [σ^2_A] were estimated using mixed model also. In early segregating populations such as F_2 and F_3, the contribution of non-genetic sources to phenotypic effects are substantial. Hence, the use of best linear unbiased predictor (BLUP), which take care of non-genetic effects, as estimates of genotypic values of plants on which data are recorded is shown to be highly effective (Lorenzana and Bernardo, 2009). The data from parents, F_1's, F_2 and F_3 were fitted to a linear mixed effects model and BLUPs of [m] and [a] were estimated using META-R (Alvarado *et al.,* 2015).

Predicting Frequency of Transgressive RILs

Assuming that the data follow normal distribution, the probability (frequency) of recovering RILs that are likely to transgress the better parent (HA 5) was estimated as standard normal distribution integrals corresponding to quotient, (mean of HA 5-m)/σ_A for each trait considered in the present study; where, [m] is mid parental valueand σ_A is square-root of σ^2_A (Jinks & Pooni, 1976; Pooni & Jinks 1978 and Jinks & Pooni, 1980). This approach to predict transgressive RILs is based on the assumption of absence of epistasis. Hence, homogeneity of phenotypic variances of F_2, F_3 and F_4 generations was examined using Levene's statistic (1960) as an evidence for presence / absence of epistasis. While significance (and hence heterogeneity of variances) of Levene's test indicate presence of epistasis, non-significance (and hence homogeneity of variances) of the same indicate absence of epistasis.

Validation of Predicted Frequency of Transgressive RILs

The material for validation consisted of 102 F_4-families derived from HA 4× HA 5. The seeds of each

of 102 F_4-families were sown in a single row of 3 m length. Ten days after sowing, seedlings were thinned maintaining 10 plants in each row with intra-row spacing of 0.20 m and 0.45 m between rows. The data were recorded on five randomly selected plants from each of the F_4-families for the same four quantitative traits for which frequency of transgressive RILs were predicted. Transgressive segregates were identified for each trait, as those F_4 plants whose BLUP values exceeded those of best parent, HA 5.The number of such F_4 segregates were counted and expressed in per cent. The observed frequency of F_4-plants that surpassed the phenotypic limits of HA 5 was compared with that of predicted to examine if observed and predicted frequency of RILs in F_4 generation were comparable for all the four quantitative traits. Narrower the difference between predicted and observed frequency of transgressive RILs, higher is the reliability and robustness of the prediction.

Results and Discussion

ANOVA of $F_{2:3}$ Families

ANOVA is a diagnostic step to detect and estimate variation attributable to target source (σ^2_A in the present study). ANOVA indicated significant differences among means of 144 F_3 families for all the traits (Table 2). Most of the genetic variation among F_3 families is predominantly contributed by genes with additive effects (van Ooijen, 1989). Hence, significant differences among the means of $F_{2:3}$ families indicate significance of $[\sigma^2_A]$ in controlling the inheritance of all the traits considered in the present study. That said, dominance, if present also contributes to $[\sigma^2_A]$. However, rather a very low magnitude and non-significant estimates of dominance (Table 2) suggest that estimates of $[\sigma^2_A]$are indeed contributed by only additive effect genes controlling all the traits. Non-significant variation in the means of F_2, F_3 and F_4 generations (Fig. 1) provide further evidence for the absence of dominance (Bernardo, 2020). Significance of $[\sigma^2_A]$ in the study is not surprising as, empirical studies across a range of crops have indicated that $[\sigma^2_A]$ contributes over 50 per cent and often close to 100 per cent to observed variation across a range of traits (Hill *et al.,* 2008 and Bernardo, 2020). Hill *et al.* (2008) and Bernardo (2020) have theoretically demonstrated that $[\sigma^2_A]$always more than

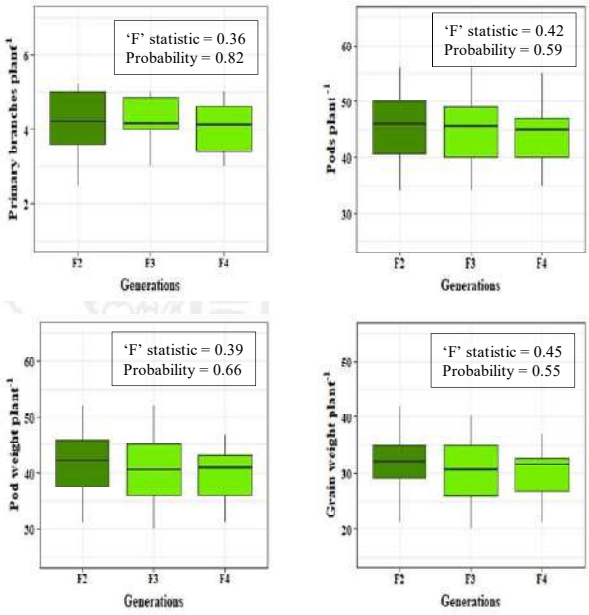

Fig. 1: Boxplots showing comparative quantitative traits means of different selfing generations derived from HA 4 × HA 5 dolichos bean cross

Table 2

Analysis of variance of $F_{2:3}$ progeny families for four quantitative traits in HA 4 × HA 5 dolichos bean cross

Source of variation	Degrees of freedom	Primary branches plant^{-1}	Pods plant^{-1}	Pod weight plant^{-1} (g)	Grain weight plant^{-1} (g)
Between $F_{2:3}$ families	143	05.59 **	89.00 **	54.25 **	67.6 **
Within $F_{2:3}$ families	01	0.22	01.17	02.12	02.22
Blocks with in replication	11	01.83	01.53	01.96	02.05
Error	132	01.83	21.10	15.20	16.32

**Significant@ P=0.01

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non-additive genetic variation even if there exists substantial interaction between alleles within each locus (dominance) and across loci (epistasis) controlling quantitative traits. In the present study, significance of [σ^2_A] is important considering that it is one of the predictors of the frequency of transgressive RILs.

Interpretation of [a] and [σ^2_A]

The quantitative genetic parameters, [a] and [σ^2_A] are the predictors of transgressive RILs that could be derived from advanced selfing generations derived from HA 4 × HA 5 cross. Being based on first-degree statistics, estimates of [a] are likely to be deflated due to internal cancellation of increasing and decreasing effect alleles at loci dispersed between the parents. However, being based on second degree statistics, the estimates of [σ^2_A] indicate true properties of additive effect alleles, as they are not affected by internal cancellation of increasing and decreasing effect alleles. Thus, genetic interpretation based on estimates of [a] alone or [σ^2_A] alone would be often misleading and may indicate different types of genetic control, which however, is illusionary. Hence, joint consideration of [a] and [σ^2_A] provide most comprehensive information on the mode of action of additive effect genes controlling the inheritance of quantitative traits (Kearsey and Pooni, 1996). In our study, while the differences between the estimates of [a] and [σ^2_A] were slightly narrow for primary branches plant^{-1}, they were substantially largerfor other three traits (Table 3). High magnitude of the estimates of [σ^2_A] and a greater difference between [a] and [σ^2_A] indicate that pods plant^{-1}, pod weight plant^{-1} and grain weight plant^{-1} are likely to be controlled by increasing and decreasing large effect additive genes that are dispersed between the parents of the cross. On the other hand, slightly higher estimates of [σ^2_A] and narrow difference between estimates of [a] and [σ^2_A] suggest that primary branches plant^{-1} is likely to be controlled by increasing and decreasing small effect additive genes that are dispersed between the parents of the cross. Our research group has earlier reported the importance of [σ^2_A] in the inheritance of pod and grain yields in dolichos bean (Keerthi *et al.,* 2015 and Chandrakant *et al.,* 2015) and in horse gram (Chandana *et al.,* 2022).

TABLE 3

Estimates of additive effects [a], mid parent value [m), dominance effects [d] and additive genetic variance [σ^2_A] for four quantitative traits in $F_{2:3}$ families derived from HA 4 × HA 5 dolichos bean cross

Traits	[m]	[a]	[d]	[σ^2_A]
Primary branches plant^{-1}	5.08	0.81 *	0.02	2.38 *
Pods plant^{-1}	48.50	5.60 **	0.12	50.01 **
Pod weight plant^{-1} (g)	43.20	5.08 **	0.26	58.01 **
Grain weight plant^{-1} (g)	27.45	3.16 **	0.30	51.28 **

*Significant @ P=0.05** Significant@ P = 0.01

Predicted and Realized Frequency of Transgressive RILs

Transgressive RILs are selected for use as pure-line cultivars in most naturally self-pollinating crops including dolichos bean. Most often than not transgenic RILs are selected from segregation populations derived from crossing parents, which themselves are often high-yielding varieties with desired traits distributed between them (as is true in the present study). If no transgressive RILs were ever found, plant breeding would not have worked in the past. Without transgressive segregation (TS), plant breeding would notwork in future as well (Mackay, 2021). Though TS occurs frequently enough that plant breeding works as a matter of routine, not all crosses display it and only a small proportion of progeny in any particular cross display TS. It is therefore, relevant to identify the potential crosses that uncover high frequency of TS.

Predicting the frequency of transgressive RILs that could be derived from advanced generationsis an objective method of identifying potential cross(es). In the present study, the frequency of transgressive RILs predicted using the predictors, namely [a], [m] and [σ^2_A] estimated based on least-squares as well as mixed-model was higher for primary branches plant^{-1} and grain yield plant^{-1} than for other two traits (Table 4). However, the frequencies of transgressive RILs predicted using the predictors estimated based

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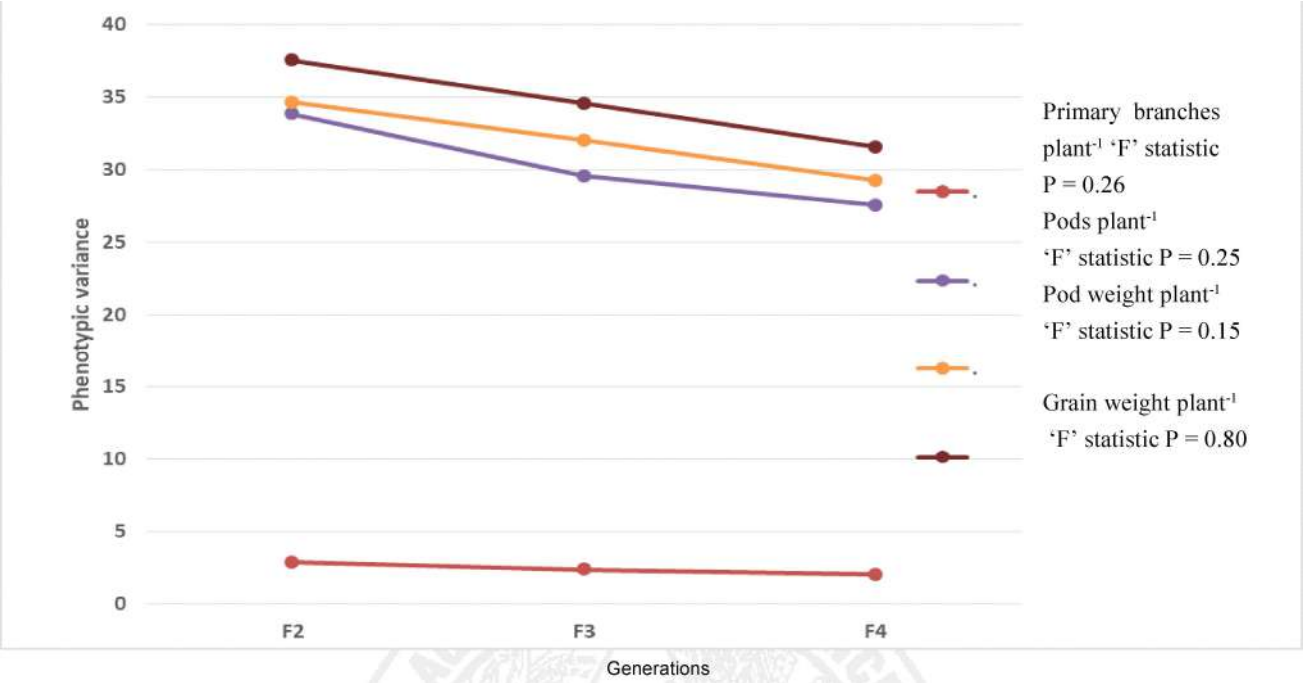

Fig. 2 : Graphs showing comparative quantitative traits' phenotypic variances in different selfing generations derived from HA 4 × HA 5 dolichos bean cross

on mixed model was slightly higher than those predicted using the predictors estimated based on traditional least square method for all the traits except primary branches plant^{-1}. Adequacy of A-D model (as indicated by non-significant joint scaling test) as well as non-significant variances of F_2, F_3 and F_4 generations (Fig. 2) (indicating lack of evidence for the role of epistasis) (Kearsey and Pooni, 1996), suggest that predicted frequencies of transgressive RILs are unbiased and hence reliable. The relative magnitudes of predicted frequency of transgressive RILs that could be derivable from F_2 of biparental crosses are often used to explain quantitative genetic basis of heterosis. This is because, this approach to explain the causes of heterosis help avoiding issues associated with the interpretation of the degree of 'dominance' or 'over-dominance' as the real cause of heterosis. The predicted probability of derivable transgressive RILs is negligible, if 'over-dominance' is the real cause of heterosis. On the contrary, if the predicted probability of derivable transgressive RILs is substantial (as is true in the present study), heterosis is due to dispersion of completely or incompletely dominant genes (additive genes in the present study as dominance is absent) between the parents (Kearsey and Pooni, 1996). It should be therefore, possible to recover RILs harboring number of favorable additive genes greater than those present in the better parent from the segregating population derived from H A 4 × HA 5 cross used in the present study.Several researchers such as Carneiro *et al.* (2002) in common bean, Chahota *et al.* (2007) in lentil, Shivakumar *et al.* (2016) in dolichos bean and Chandana *et al.* (2022) in horse gram have also predicted the frequency of transgressive RILs using the predictors estimated based on least square method and the predictions were unbiased and reliable. Meszzomo *et al.* (2021) in wheat predicted the frequency of transgressive RILs using the predictors estimated based on both least square method and mixed model and reported better predictability of the latter.

The potential argument against our results would be that the predicted frequency of transgressive RILs is likely to be biased in the presence of linkage disequilibrium (LD) between the pairs of genes controlling traits investigated in the study. Quantitative genetic theory indicates that LD has no effect on the

estimates of [a] (one of the predictors of RILs used in the study). However, generally LD biases [σ^2_A]. While coupling phase of linkage inflates, repulsion phase of linkage deflates [σ^2_A]. However, estimates of [σ^2_A] obtained from F_3 ANOVA are closer to those obtained from RIL population and hence predictions would be reliable even in the presence of LD (Kearsey and Pooni, 1996).

A fairly good agreement between predicted (in F_3 generation) and realized (in F_4 generation) frequency of RILs that transgressed HA 5 for all the traits (Table 4) suggested reliability of approach used in our study to predict the frequency of transgressive RILs. Several researchers such as Carneiro *et al.* (2002) in common bean, Chahota *et al.* (2007) in lentil, Shivakumar *et al.* (2016) in dolichos bean and Chandana *et al*. (2022) in horse gram have also reported a good agreement between realized and predicted frequency of transgressive RILs. Thus, our results and those reported by researchers in other legumes provide evidence for the robustness of the method of predicting the frequency of transgressive RILs from bi-parental populations. We therefore believe that this method of predicting the frequency of transgressive RILs could be reliably used as an objective criterion to assess the breeding potential of the crosses and to identify best ones from among a large number of crosses routinely developed in crop breeding programmes.

Both quantitative genetic theory and empirical results indicate that TS mostly results from the combinations of complementary 'plus' and 'minus' alleles dispersed between parents (Powell & Thomas, 1992; Surma *et al*., 1998; Rieseberg *et al.,* 1999 and Surma *et al.,* 2000). That is, individuals that receive 'plus' alleles from both parents or 'minus' alleles from both parents are likely to exhibit extreme phenotypes. Thus, TS most likely to occur when difference between the parents is small and [σ^2_A] is high as is true in our study. This is possible when both the parents are phenotypically similar but genetically diverse. TS is also attributed to 'Ommigenic' theory, according to which, TS occurs through synergistic interaction between relatively fewer major effect 'core genes' and the more numerous but minor effect 'peripheral genes' scattered throughout the genome (Boyle *et al.,* 2017 and de Los Reyes, 2019).

Breeding Implications

It is possible to accelerate the process of identification of new crop cultivars with a desired combination of both farmer and end-user preferred traits in breeding populations that are predicted to result in high frequency of transgressive RILs (Kochetov *et al*., 2021). However, genotypes that fall short of maximum trait expression are relatively common in segregating populations routinely developed by crop breeders (Bernardo, 2020). This is because, appearance of genotypes with most, if not all the desirable genes controlling quantitative traits' requires several precisely placed cross overs between all possible pairs of desirable and un-desirable genes linked in repulsion phase in all the chromosomes (Witcombe *et al.,* 2013 and Bernardo, 2020). However, the chance of

TABLE 4

Predicted and realized frequency of RILs which transgressed the limits of better parent (HA 5) for four quantitative traits in HA4 × HA5 dolichos bean cross

Trait	Predicted frequency of RILs ≥ HA 5 based on least square estimates of predictors	Predicted frequency of RILs ≥ HA 5 based on BLUP estimates of predictors	Realized frequency of RILs ≥ HA5
Primary branches plant^{-1}	25.50	22.50	28.98
Pods plant^{-1}	17.90	18.05	13.25
Pod weight plant^{-1}(g)	12.50	15.00	09.56
Grain weight plant^{-1}(g)	26.44	27.20	24.51

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occurrence of such precisely placed cross overs in high frequency is almost remote. It is therefore, logical to hypothesize that different genotypes harbor different combinations of favourable and unfavourable alleles. Nevertheless, crossing among such genotypes (falling short of maximum trait expression) selected from the same cross is expected to uncover relatively higher frequency of genotypes with near-maximum trait expression even from small F_2 / $F_{2:3}$ populations that breeders routinely handle (Bernardo, 2020). Our previous reports indicate that it is possible to increase the frequency of TS by one or more cycles of random mating between F_2 individuals resulting from biparental crosses in dolichos bean (Chandrakant *et al.,* 2015). Thus, based on our results and those reported by other researchers, we believe that using large-sized populations derived from a few productive crosses selected based on an objective criterion such as the one used in our studyis likely to increase the probability of recovering transgressive RILs in inbreeding crops such as dolichos bean.

The method of assessing the breeding potential of crosses at early segregating generations based on the predicted probability of transgressive RILs that could be derived in advanced breeding populations sounds practical as breeders develop F_2 / $F_{2:3}$ populations from many crosses on a routine basis. Our results indicate that there is no reason why crop breeders ever need to go beyond $F_{2:3}$ generation of cross if the transgressive RILs is predicted to be low.

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