Advanced Science and Technology Letters
Vol.120 (GST 2015), pp.850-857
http://dx.doi.org/10.14257/astl.2015.120.166

Comparisons of various generations of the synthetic populations

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Abstract. Both selection and competition are expected to influence the composition of the advancing generations of the population. Further their effects are normally cumulative such that the latter generations are more influenced than the early ones (relative to S_0). Therefore selfed samples of S_1, S_2, and etc. generations of the population are not only expected to differ from the S_0 which is the base population but they may also differ from each other. The overall means of various generations within the B and D synthetic populations were compared to determine the pattern of differences that may exist between them.

Key words: Selection, competition, generations, synthetic populations.

1 Introduction

Monitoring of the B and D synthetic populations has continued over the past twenty or so years. Boughey (1978) initiated these investigations by comparing the phenotypic distributions of the S_0, S_1 (or S_2) and F_2 generations of each population. Roy (1983) Douglas (1982) and Al-Banna (1983) followed her by carrying out similar experiments with large samples of the S_4 and S_5 generations of the B and D populations. Roy (1983) also proposed a method for estimating the heterozygosity levels for metrical traits which he applied to the S_4 generation of D population. The same procedure was later employed by Bourne (1986) and by us to determine the heterozygosity levels I the S_6 and S_7 generations of the B population. These investigations revealed that some permanent changes has occurred in both populations. It was further shown that a large portion of these changes were due to the introduction of heterozygosity which was produced by the natural breeding system of *Nicotiana rustica*. Significant differences attributable to selection/competition were also detected in all the experiments but these results were not observed to be consistent throughout. On one or two occasions the effects of selection were in fact observed to oppose each other and this was interpreted to indicate that populations and approached some sort of equilibrium (Roy, 1983, Anssour et al, 2009). An alternative albeit more plausible explanation of the above results, however, could be that the selection is not entirely directional and the optima are shifting between environments. Genotype environment interactions may also have reinforced the differences between various assessments and made the results differ vilely. Present study was therefore

ISSN: 2287-1233 ASTL

conducted to assess the true magnitude of changes that may have occurred in the advancing generations of either population and visualize any trends that may exist between them. The first assessments were carried out by taking large random samples of individual from various S_n generations and comparing the performances of their selfed progenies in a single macro environment. In the second set of experiments the distributive properties of the S_0 and the F_∞ S_n generations were compared.

2 Material and Methods

This investigation involved two experiments which were conducted to compare all available generations of each synthetic population. One hundred selfed families of each of the $S_1(F_2S_1)$, $S_2(F_2S_2)$ etc. generations were assessed with the parental, F_1, F_2 and S_0 generations. Seeds of these families were produced by raising 100 randomly chosen plants from each generation and selfing them. Individual plants of 82 B and 60 D lines were selfed. These samples were boosted to 100 families by adding inbreds derived from other independent inbreeding programs. The parental (P_1, P_2), F_1 and F_2 generations of each ancestral cross (V_1x V_5 and V_2 x V_{12}) were also produced. The scored traits are as follows: H6 (plant height six weeks after sowing), H7, LL (leaf length), FT (flowering time), HFT (height at flowering time), and PH (plant height).

3 Results and Discussion

3.1 Comparisons of F_2S_1, F_2S_2 and F_2S_n means

One way analysis of variance was used to determine the significance of differences between the overall means of the selfed progenies of S_1, S_2, …, S_n generations. It took the following form:

Item	df	M.S.	V.R.
Between generations	n-1	MS_1	MS_1/MS_2
Within generations	$N(n_1\text{-}1)$	MS_2	

Here n and n_1 stand for number of generations and number of families/within generations, respectively.

The between generations sum of squares (for n-1 df) when significant were subjected to further partitioning to pinpoint the source(s) of variation amongst generations. Um of squares due to each degree of freedom was obtained by applying the following orthogonal comparisons:

Source of variation Generations

	F_2S_1	F_2S_2	F_2S_3	F_2S_4	F_2S_5	F_2S_6	F_2S_7	…F_2S_n
F_2S_1 vs F_2S_2	1	-1	0	0	0	0	0	… 0
F_2S_1 vs (F_2S_1 + F_2S_2)	1	1	-2	0	0	0	0	… 0
F_2S_1 vs (F_2S_1 + F_2S_2 + F_2S_3)	1	1	1	-3	0	0	0	… 0
F_2S_1 vs (F_2S_1 + F_2S_2 + F_2S_3 + F_2S_4)	1	1	1	1	-4	0	0	… 0
F_2S_1 vs (F_2S_1 + F_2S_2 + … + F_2S_5)	1	1	1	1	1	-5	0	… 0
F_2S_1 vs (F_2S_1 + F_2S_2 + … + F_2S_6)	1	1	1	1	1	1	-6	… 0
F_2S_1 vs (F_2S_1 + F_2S_2 + … + F_2S_{n-1})	1	1	1	1	1	1	1	… -(n-1)

The actual SS were however computed as follows because total sizes often varied between generations.

$$SS\ [S_n \text{ vs } (s_1+s_2+ \ldots. +s_{n-1})] = \frac{\left(\sum_{j=1}^{n-1} GT_j\right)^2}{\sum_{j=1}^{n-1} N_j} + \frac{GT_n{}^2}{N_n} - \frac{\left(\sum_{j=1}^{n} GT_j\right)^2}{\sum_{j=1}^{n} N_j}$$

Here, GT_j and N_j stand for the grand total and the total number of individuals in the jth generation.

Each component was tested against the within families mean squares by F test.

Results of comparing the overall means of the F_2S_1, F_2S_2 etc progenies of B population and the one way analysis of variance are not given. The results of one way analysis of variance showed that the seven sets of families differed significantly from each other for all traits except H_6, therefore, at least five traits seem to display differential influences of agents like selection and competition as well as of the breeding system. Partitioning of the between generations SS further revealed that most of the differences were contributed by the F_2S_5, F_2S_6 and F_2S_7 means. They differed from each other and from F_2S_1, F_2S_2, F_2S_3 and F_2S_4 for LL, FT, HFT and FH while the latter did not differ from each other for any of these traits. All the significant differences in the H7 and some in FH, on the other hand, were contributed by the differential performance of $\overline{F\ {}_2S_3}$, while the rest of the generations had very similar means. The same analyses were performed on the overall means of the various generations of D population (results not shown). Once again the mean performances of the six sets of families are observed to differ significantly for H_6, H_7, and FT. Therefore at least three characters seem to be differentially affected by the agents of change. Further, F_2S_5 and F_2S_6 are the major sources of these differences and only in one case have the other generations (e.g. S_1 and S_2) shown marginally significant differences for FT.

3.2 Comparison between S_0 and (F_2S_1 to F_2S_n) generations

Average performances of all the selfed families derived from the n generations of population ($\overline{F_2S}$) was also compared with the mean of the base population (S_0) to determine if a consistent shift has taken place in the synthetic population. Standard "t" test was used to determine the significance of these differences. The results are presented in table1 for the B population, however for the D population were not shown.

Table1. Comparison between S_0 mean and the overall mean of all the F2Sn generations of the B population.

character	$\overline{S_0}$	$V_{\overline{S_0}}$	$\overline{F_2S}$	$V_{\overline{F_2S}}$	C	Significance
H_6	23.53	0.4772	23.55	0.0522	-0.027	n.s.
H_7	42.03	1.0024	42.71	03163	-0.592	n.s.
LL	17.99	0.0737	19.44	0.1355	-3.170	**
FT	29.38	0.6488	31.51	0.7149	-1.824	n.s.
HFT	61.32	2.4845	67.65	5.3062	-2.268	*
FH	114.12	2.5095	121.09	6.8060	-2.284	*

In B population, the $\overline{F_2S}$ is observed to be significantly larger than S_0 mean for LL, HFT and FH. Difference in the D population, However, are in the opposite direction and $\overline{F_2S}$ is in fact significantly similar than S0 mean (results for the D population was not shown).

3.3 Tests of selection and competition at means level

As mentioned earlier, the observed changes in the overall means of progeny families of S_1, S_2… S_n generations could have occurred due to the interjection of heterozygosity and/or the effects of selection and competition. The estimates of β_n and C_n values of the various generations of B and D populations that were obtained by Roy (1983) and Bourne (1986) and have been used in the model fitting (results not shown). It is implied that the same models will fit the ancestral as well as the descendent generations when the synthetic population is not subjected to any directional selection and competition. Models which fit satisfactorily to the means of P_1, P_2, F_1, F_2 generations of the V_1 x V_5 cross and the S_0 generations of the B population are summarized in table2. The additive component ([d]) was detected to be significant for H_6, H_7 and LL but not for the rest of traits; the dominance component ([h]) was significant for H_6, H_7, LL and FH and the additive x additive interaction ([i]) was non-significant for all traits except LL. Dominance x dominance interaction ([l]) was non-significant throughout. Parameters of these models were then fitted to the overall means of P1, P_2, F_1, F_2, $S_{0\ \text{and}}$ F_2S_1 generations for each traits and the difference between the new χ^2 and pervious one obtained. This provided χ^2 with one degree of freedom and its significance determined if the same model failed to fit all generations of the synthetic population. The F_2S_1 mean was then (successively) replaced by the means of F_2S_3 and F_2S_7 and new $\chi^2_{(1)}$ values obtained (the remaining generations were left out because estimates of β_n and C_n were not available for them). The three $\chi^2_{(1)}$ values were then added to obtain a single $\chi^2_{(3)}$ value which show that

$\chi^2_{(3)}$ is significant for LL, FT, HFT and FH but not for H_6 and H_7. This shows that selection/competition has affected the mean of F_2S_n scores significantly for all characters for all characters except H_6 and H_7(results not shown).

Table2. Components of the first degree statistics obtained from the P_1, P_2, F_1, F_2 and S_0 generations of the V_1 x V_5 cross by weighted least squares analysis.

Components	H_6	H_7	LL	FT	HFT	FH
m	23.63±.69	42.15±.99	17.23±..24	28.64±.66	62.45±1.37	114.07±1.56
[d]	3.48±1.41	4.45±2.24	1.61±.61	–	–	–
[h]	6.40±2.14	10.85±3.61	3.54±.87	–	–	10.51±5.12
[i]	5.75±1.56	9.15±2.45	–	-5.49±- 1.36	-12.97±2.74	–
[l]	–	–	–	–	–	
$\chi^2_{(d.f.)}$	0.76 (1)	0.67 (1)	0.21 (2)	3.03 (3)	3.67 (3)	2.11 (2)
Sig.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

3. 4 Comparison of V_{F2S1}, V_{F2S2}… and V_{F2Sn}

Total variances (V_{F2Sn}) of the F_2S_1, F_2S_2… F_2S_n generations were initially compared to determine if they differed from each other. A Bartlett's test to homogeneity was used to test the significance of difference between them. Further the following comparisons were also made to pin-point the level of differences that were displayed by a particular set of generations.

(1) F_2S_2 vs F_2S_1
(2)F_2S_3 vs (F_2S_1 + F_2S_2)
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.
.
(n-1)F_2S_1 vs (F_2S_1 + F_2S_2 + … + F_2S_{n-1})

Significances of each of these comparisons were determined by 'C' test which was calculated as $\sqrt{2}\ \chi^{2}$ - $\sqrt{2df-1}$ following Fisher and Yates (1963). In B population the total variance of various generations differ significantly for FT and HFT (results not shown). $\chi^2_{(5)}$ values are also observed to be significant for H_6, LL and HFT in the D population, indicating that the total variances of various generations also show significances for these traits (results not shown). Orthogonal comparisons of the total variances of various generations revealed that F2S4 and F2S7 generations were largely responsible for the above differences in the B population (results not shown). The situation in the D population was, however, much more complex and up to five generations were observed to show significant differences for various traits (results not shown).

The results of comparison between the pooled variance of all selfed families of n generations of a population (V_S) and total variance of its S_0 generation show no indication of any clear shift in the variances (results not shown). In the most cases the two variances are very similar to each other and they differ highly significantly only for H_6 in both populations. Further V_{S0} is larger than V_S for this trait in both cases.

3. 5 Comparison of between families' components

Because the S_0 generation of each population consisted of inbred lines which were derived by single seed descent, its genetic component σ^2_b has an expectation of D (additive genetic variance). In the advancing generations, however, the genetic variance will be equal to D only when there is no selection, competition and out crossing. Introduction of heterozygosity as well as selection and competition will make the genetic variation of the selfed families of the populations differ from D. If there were no selection and competition it would be modified to $(1-\beta_n)$ D + 1/4 $\beta_n(1-\beta_n)$H, due solely to the effects of out crossing. Model fitting was employed to compare σ^2_b's of various generations. The model used to compare the between families components (σ^2_b) of the F_2S_1 … F_2S_n generations of a synthetic population and that of S0, F_2S_1 … F_2S_n are given in tables 3 and 4, respectively.

Table3. Model used to compare the between families' components (σ^2_b) of the F_2S_1 … F_2S_n generations of a synthetic population.

Generation	Mean square	σ^2_{w1}	σ^2_{w2}	σ^2_{wj}	σ^2_{wn}	σ^2_b
F_2S_1	Bet. fams.	1	0	0	0	r_1+
	With. fam.	1	0	0	0	0
F_2S_2	Bet. fams.	0	1	0	0	r_2
	With. fam.	0	1	0	0	0
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.						
.						
F_2S_i	Bet. fams.	0	0	1	0	r_i
	With. fams.	0	0	1	0	0
.						
.						
.						
F_2S_n	Bet. fams.	0	0	0	1	r_n
	With. fams.	0	0	0	1	0

+r1, r2, etc. stand for the effective family size of each generation

Table4. Model used to compare the between families' components (σ^2_b) of the S_0, F_2S_1 … F_2S_n generations of a synthetic population.

Generation	Mean square	σ^2_{w0}	σ^2_{w1}	σ^2_{w2}	σ^2_{wj}	σ^2_{wn}	σ^2_b
S_0	Bet. fams.	1	0	0	0	0	r_0
	With. fam.	1	0	0	0	0	0
F_2S_1	Bet. fams.	0	1	0	0	0	r_1
	With. fam.	0	1	0	0	0	0
F_2S_2	Bet. fams.	0	0	1	0	0	r_2
	With. fams.	0	0	1	0	0	0
.							
.							
.							
	Bet. fams.						
F_2S_i	With. fams.	0	0	0	1	0	r_i
		0	0	0	1	0	0
.							
.							
.							
	Bet. fams.						
F_2S_n	With. fams.	0	0	0	0	1	r_n
		0	0	0	0	1	0

In the first model (n+1) parameters were fitted to (2n) statistics. So it provided a chi-square of goodness of fit for (n-1) degree of freedom and its significance determined if σ^2_b differed between F_2S_1 … F_2S_n generations. In the second model, there were (n+2) parameters and (2n+2) mean squares. Therefore it provided a χ^2 with n degrees of freedom. While this model tested the adequacy of a common σ^2_b to all the generations the difference between this and the above χ^2 for (n-1) df provided a $\chi^2_{(1)}$ value whose significance determined if $\sigma^2_{b(S0)}$ differed significantly from the pooled σ^2_b of the other generations. Results of the above mentioned model fitting (results not shown) showed that differences between σ^2_b 's of various generations are not significant for any traits in the D population (results not shown) and for all except H_6 in the B population. Further, in no case is $\chi^2_{(1)}$ highly significant suggesting that the average σ^2_b of various F_2S_n generations does not differ from the between families component of the S_0 generation.

Investigations of the source(s) of differences between the σ^2_b's of various F_2S_n generations for H6 in the B population revealed that $\sigma^2_{b(F2S7)}$ differed significantly from the rest (it is larger than the rest of σ^2_b's).

3. 6 Comparisons of within families' components

Within family variances of various generations were compared by Bartlett's test. Initially, σ^2_w of F_2S_1, F_2S_2 … etc. were compared to determine if they differed significantly from each other. Then their pooled average was compared with the $\sigma^2_{w(S0)}$ to test if there was a significant difference between them. Then $\chi^2_{(n-1)}$ obtained from the comparison of the F_2S_1, F_2S_2 … F_2S_n generations was further partitioned into (n-1) chi squares (for one degree of freedom each) with a view to determine the true source of differences. However, these analyses were only when $\chi^2_{(n-1)}$ was observed to be significant. The χ^2 values pertaining to the above described tests are presented for the B synthetic population (results not shown). It shows that σ^2_w's of the F2S1 … F2Sn generations differ significantly for four characters namely, H_7, FT, HFT and FH. Further, these differences are exclusively attributable to the σ^2_w of F_2S_7 generation which is significantly smaller than the pooled σ^2_w of the remaining (F_2S_1 to F_2S_6) generations. There is however no difference between the pooled σ^2_w of these (F_2S_1, F_2S_2 … F_2S_n) generations and that of the S_0 generation for any trait. Within family variances of the F_2S_1 … F_2S_6 generations of D population also differ significantly for all traits except LL (results not shown). In this case, however, F_2S_5 to F_2S_6 generations are the major sources of differences because their σ^2_w's are much smaller than those of the rest of generations. The situation is, however, much more complex in the case of HFT where $\{\sigma^2_{w(F2S3)} \approx \sigma^2_{w(F2S4)}\} > \{\sigma^2_{w(F2S1)} \approx \sigma^2_{w(F2S2)}\} > \{\sigma^2_{w(F2S5)} \approx \sigma^2_{w(F2S6)}\}$ (results not shown).Whithin families component of the S_0 generation, on the other hand, is significantly smaller than the pooled σ^2_w of the F_2S_1 … F_2S_6 generations for LL and the reverse is true ($\sigma^2_{w(S0)} >$ mean σ^2_w) for H_6 (results not shown).

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