

PUNJAB AGRICULTURAL UNIVERSITY

Dr. A.K. Gupta,
Associate Prof: of Plant Breeding.

D.O. no. 5386

Ludhiana
Dated March 7, 1967.

Respected Dr. Swaminathan:

Thanks for your letter and also for writing to N.R.C.
I am enclosing herewith the revised manuscript alongwith both the reports.
All the changes suggested in first report have been done, while about
second report, I can say as given under, point to point:-

(1) Presentation and analysis

- (i) and (ii). Required information given.
- (iii) - It is not possible to give more details as it will increase the number of tables, because to give analysis of variance for each will need twelve more tables. For the purpose of knowing significance, C.D. values are given.
- (iv) - I think, there is no harm in giving F-values, but if you like, treatment mean squares for each may be given in place of 'F'. This will be with you in the analysed data. *Figure 1 may be modified as suggested by referee.*
- (v) - This seems to be serious objection, to me. You please decide whether to keep Delhi data or not.

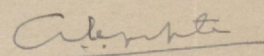
(2) Interpretation

- (i) - There is no need to prove the homozygous nature of tetraploids, it is only expected as discussed. It will be desirable if it can be said that tetraploids were obtained from a few plants of T 22.
- (ii) - It can be either way, but "recombination" is better than "segregation".

Please see these and finalise. I would like to have a copy of the final manuscript, as soon it is done.

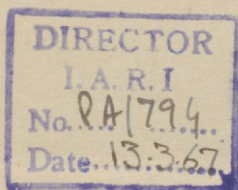
With respects and regards,

Sincerely yours,


(A.K. Gupta)

Dr. M.S. Swaminathan,
Director,
I.A.R.I.,
New Delhi - 12.

...



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RADIATION BOTANY

Referee Report Form

PLEASE RETURN SIGNED ORIGINAL AND UNSIGNED CARBONS (2)

Author **A.K. Gupta and M.S. Swaminathan**

Title **Induced Variability and Selection Advance for Branching in Auto-tetraploids of Brassica campestris var. Toria**

Referee's report

The subject of the work is original and the paper interesting, quite suitable to be published in the Journal.

to improve the ms. the only suggestions are the followings:

- 1) Abstract, 15th row: Selection norms are quoted, but not specified; it seems advisable to specify what method and pressures of selection have been used.
- 2) page 3: 2nd row from the bottom: selection in plus direction is described, but no indication is given of the selection pressure used, which is important for evaluating the progress of selection.
- 3) page 5: 12 row: it is much better to specify "minus direction" than "direction".

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The authors have written a useful and interesting paper on a topic suitable for publication in "Radiation Botany". Several aspects of the paper need further attention, however, and the authors may like to consider the following points:-

(1) Presentation and analysis of the data

(i) Many readers will be unaware of the agricultural use of "toria" and therefore the significance of increasing the total weight of seeds per plant.

(ii) It is not made sufficiently clear what data come from what selection procedure. The sentence on page 3 (last 3 lines) indicates one selection procedure and page 4 (first few lines) indicates another. Does the M_3 data in Table 1 come from families selected in the first or second way?

(iii) More details of the M_2/M_3 data and its analysis are desirable. Variances between progenies within each dose group with regard to plot means and transformed variances should be given in Table 1, and also the variances between replicates. Alternatively the results of an analysis of variance should be given. It is essential to indicate the significance of the results in Table 1.

(iv) The actual data rather than F-values are needed in Table 2. Why were the data from the two dose groups pooled, and is this justified statistically? If the actual means and variances are not given in an expanded Table 2, they should be presented in an expanded Figure 1, keeping the dose groups separate. *Since the variances from the two doses were not significantly different, the 2 dose groups have been pooled.*

(v) Control data from the Delhi location should be included in Table 3, otherwise all of the Delhi results omitted. (How can soil alkalinity affect the control but not the other families in a randomised experiment? - the reader will want to know.) It is certainly not true to state, on the basis of the results given in Table 3, that the 96 Kr family was superior to the control in all three locations (bottom of page 4). Standard errors or details of an analysis of variance should be given for the results in Table 3.

(2) Interpretation

(i) The authors point out that the diploid parent of the autotetraploid was almost certainly highly heterozygous, but suggest that the control tetraploid material used in the experiment was not (top of page 8). This point is crucial for their interpretation and needs to be elaborated, preferably with data to support this contention. Unless it can be clearly demonstrated, either by selection or genetic analysis, that the control material was nearly homozygous, the conclusion that the selection response was due to induced mutation cannot be supported. It is not enough to show that selection response was greater in irradiated than in control families, since radiation-induced pseudorecombination,

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chromosome loss, etc., may occur. If satisfactory evidence cannot be given, such of the discussion is inappropriate. The potential practical value of the work is of course unaffected by this uncertainty in the origin of the induced variation.

(ii) Why is recombination (rather than segregation) suggested on page 7, line 6?

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INDUCED VARIABILITY AND SELECTION ADVANCE FOR BRANCHING
IN AUTOTETRAPLOIDS OF Brassica campestris var. Toria

A.K. Gupta* and M.S. Swaminathan,
Atomic Energy Laboratory, Indian Agricultural
Research Institute, New Delhi

ABSTRACT:

Autotetraploids of Brassica campestris var. toria ($2n = 4x = 40$) were produced at the Indian Agricultural Research Institute in 1941 through colchicine treatment in the diploid strain T.22. The seed fertility of the autopoloid was initially very low but was brought to the level of the diploid through the mass pedigree system of selection. In spite of the improved fertility and also larger seed size, the yield of the autopoloid did not exceed that of the diploid, owing to a reduction in the ability to produce secondary and tertiary branches. Hence, seeds of an 'evolved' autopoloid culture belonging to the C_{19} generation were exposed to 96 and 128 Kr of X-rays in 1960. A biometrical study of progeny means and variances was conducted in the M_2 and M_3 generations. Selection norms for secondary branch number were fixed and the selected plants were allowed to inter-cross. Recurrent selection was practised in the M_4 , M_5 and M_6 generations. An yield trial comparing the selected bulks from the treated and control families was conducted at three locations during 1965-66. The results indicated that (a) the variance for secondary branch number was enlarged in the M_2 and M_3 populations, while the means were not affected, (b) there was a positive selection advance for branch number during the M_3 , M_4 and M_5 generations and (c) true-breeding tetraploid cultures with a significantly higher number of secondary branches could be established. Thus, the poor branching ability of the autopoloid population could be remedied and promising tetraploid cultures developed.

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INTRODUCTION

Polyploidy was induced in Brassica campestris var. toria Duth & Full. ($2n = 20$, strain T.22) in 1941 at the Indian Agricultural Research Institute, New Delhi, by RAMANUJAM and DESHMUKH.⁽¹⁹⁾ The raw tetraploids ($2n = 4x = 40$) had a low seed fertility but through the introduction of the mass pedigree system of selection, the fertility of the autotetraploids was brought almost to the same level as the diploids.^(17,18) Coincident with the increase in fertility, the multivalent frequency registered a drop.⁽²³⁾ In spite of the great improvement in the number of seeds per siliqua in the 'evolved' autotetraploids and also the larger size of seed in them, they yielded less than the diploids in yield trials. An analysis of the causes for the lower yielding potential of the autotetraploids showed that the tetraploids had a significantly lower number of secondary and tertiary branches per plant.⁽²⁾ Thus, while gaining in seed fertility, there has been a loss in branching ability. The evolved autotetraploids in the C_{19} generation showed very little variability for the number of the primary and secondary branches per plant and hence offered little scope for selection. Since radiations can induce variations in polygenically determined traits, it was considered worthwhile to irradiate the evolved tetraploids, screen the population for variability for the number of secondary branches and assess the scope for making selection advance for this trait.

MATERIAL AND METHODS

Seeds from a single open pollinated plant of tetraploid toria were taken and were irradiated with 96 Kr and 128 Kr of X-rays. For these treatments, a

Phillips X-ray machine was used, operating at 50 kV, 2ma, without filter, at a dose rate of 16 Kr per minute at a distance of 2cm. Seeds arranged in a single layer were exposed for different durations of time depending upon the dose. Control and treated seeds were allowed to germinate in pans and three week-old seedlings were transplanted in the field in rows 1.5 ft. apart with one foot inter-plant distance. For raising the M_2 generation, M_1 plants from each treatment were selected at random and their progenies were grown in a Randomised Complete Block design with three replications, in 12 ft. long rows, 1.5 ft. apart with one row per progeny in each replication. A similar layout was adopted for comparing M_3 progenies. Data on the number of primary and secondary branches were taken from 10 plants chosen at random in each progeny both in the M_2 and M_3 generations. The progeny mean and variance (plot variance) were calculated and statistical analysis was done on these means and variances. Means were analysed according to the randomised block design analysis and F-values were calculated. For the plot variances of each progeny, the following transformation was used:

$$(n_i - 1) \log_e s_i^2 \quad \text{where } s_i^2 = \text{plot variance}$$

$$\text{and } n_i = \text{number of plants on which } s_i^2 \text{ is calculated}$$

These transformed values were then subjected to an analysis of variance and F-values were calculated. The plant progenies which were significantly superior to the control in plot mean and plot variance were selected for being carried forward to the next generation.

In the M_2 and M_3 generations, an elite bulk of single plant selections, having 20 and more secondary branches was made in each treatment as well as the control. In M_4 the genotypes with high branch number in each treatment group, were sown in isolation and allowed to intercross. This seed was carried to the next generation and this procedure was also followed in the M_5 generation. Finally at M_6 , the selected bulks from each treatment were tested for branching ability at three different locations. A randomised block design with four replications was adopted for these trials.

RESULTS

The observations on population means and variances in the M_2 and M_3 generations are summarised in Table 1. The mean values did not change but the variance was enlarged, especially for the number of secondary branches. This increase was more pronounced in M_3 , particularly in the 96 Kr treatment. The analysis of variance carried out on plot means and plot variances in each generation revealed significant differences between control and irradiated progenies. F-values for secondary branch number were significant at 1% level both for plot means and plot variances (Table II). Following selection, the mean number of primary and secondary branches increased (Fig.1). The increase was marked in the M_5 population.

The relative performance of the elite bulks in the M_6 generation at three different locations revealed that a family derived from 96 Kr treatment was superior in secondary branch number at all the locations (Table III).

The number of siliquae per main shoot and the number of seeds per siliqu^{ae}~~ae~~ were either the same as in the control population, or a little higher.

DISCUSSION

Following the reports of CLAYTON AND ROBERTSON⁽⁸⁾ and BUZZATI-TRAVERSO and SCOSSIROLI⁽⁷⁾, many studies have been conducted on mutagen-induced enlargement of variability for polygenically determined characters (see review by SCOSSIROLI⁽²⁰⁾). In most of these studies it has been observed that the mean of the irradiated population either remains unchanged or is altered in the ^{minus} direction. The variance in contrast is significantly increased in comparison with the control for the particular character studied. The present findings are in agreement with this general trend. While the population means did not change significantly after irradiation, the variances were significantly increased. In the M₃ generation, the variance was of a higher order than in the M₂ generation, particularly in the 96 Kr treatment. BHATIA AND SWAMINATHAN⁽⁴⁾ in hexaploid wheat and KOO⁽¹³⁾ in hexaploid oats have also reported that the increase in variance is more in the M₃ generation in comparison with M₂. KAO et al.⁽¹¹⁾ observed in rice a greater increase in variance in the M₃ generation and constructed formulae to calculate the radiation-induced genetic variance expected in the M₂ and M₃ generations. Their studies reveal that the fixable part of the variance is more in the M₃ generation. Similar results have also been reported by KONDO¹². LAWRENCE⁽¹⁴⁾ found a significant increase in the additive and dominant components in irradiated populations of Arabidopsis thaliana for flowering time.

Increase in the genetic variability is caused by the occurrence of extreme types, both on the positive and negative sides of the mean value. Therefore, it should be possible to shift the mean in any direction through artificial selection. OKA et al. (16) observed in irradiated material of rice that selections for plant height and heading date were equally effective in both directions. However, BATEMAN (3) in a re-interpretation of OKA's data concluded that the altered mean and variance arise from mutations in one direction. He further remarked that there is excess of mutations in the positive direction for most of the quantitative characters. BHATTIA and VAN DER VEEN (5) also reported that selection led to a shift in the mean value for maturity period only in the positive direction in EMS-treated Arabidopsis thaliana. BROCK (6) proposed the hypothesis that in species which have previously been subjected to breeding and selection, random mutations would result in an increase in variance and a shift in the mean in a direction opposite to that of the previous selection history. GAUL and AASTVEIT (9) did not agree with this hypothesis of BROCK and suggested that random mutations result in a change of the mean in a direction associated with reduced vitality. Thus, the alteration of the mean would be largely independent of the genotype used for the mutagenic treatment.

In the present investigation it was possible to shift the mean for secondary branch number towards the positive side in tetraploid toria, after recurrent selection in the 96 Kr treated population. Induction of variability must be followed by selection in order to shift the mean value of a quantitative character.

BROCK⁽⁶⁾ pointed out that the mean value for a character also moves away from the direction of previous selection; hence, selection must be applied to stabilise the mean at a desired level. The present data provide evidence in support of the effectiveness of promoting cycles of recombinations within the selected lines. Mutagenic efficiency as applied to polygenic traits should be measured not by the induced variance but by the selection advance rendered possible.

Polyploidy, by virtue of the buffering effect caused by gene and segmental duplications, has been a favourable feature in mutation breeding (15,21,22). In autopolyploids, recessive mutations are expressed more readily in M_3 and later generations than in the M_2 ⁽²¹⁾. So far, no data on the induction of mutations for polygenic traits in autopolyploids are available. The present study suggests that autopolyploids are not only suitable for the recovery of mutations in qualitative characters but also in quantitative traits.

Mutation breeding has until now been largely confined to the improvement of self-pollinated crops. This is due to the difficulties inherent in allogamous plants in distinguishing between induced mutations and the release of the variability already present⁽¹⁰⁾. Nevertheless, some improvement has been made through mutation breeding in cross-pollinated crops like Sinapis alba. Toria is a self-incompatible crop and diploid and auto-tetraploid toria are cross incompatible. The tetraploid population, derived from a single original diploid strain could obviously undergo mating only within

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Table I
Average Means and Variances in Control and
Irradiated M_2 and M_3 progenies of tetra-
ploid toria

Treatment	Total no. of progenies	Primary Branches		Secondary Branches	
		Average Mean	Average variance	Average Mean	Average variance
<u>M_2 generation</u>					
Control	21	6.54	4.02	9.24	14.93
X-ray, 96 Kr	78	6.48	3.86	9.24	26.47
X-ray, 128 Kr	72	6.38	3.28	8.77	23.95
<u>M_3 generation</u>					
Control	15	6.89	5.88	6.49	24.37
X-ray, 96 Kr	66	6.71	6.73	6.64	31.03
X-ray, 128 Kr	60	6.55	5.98	6.38	29.73

Table 2
Analysis of plot means and plot variances in M_2 to M_6
generations of tetraploid Toria

Character	Generation	F-value (Means)	F-value (Variance)
Primary Branches	M_2	2.61 **	1.88**
" "	M_3	1.59	1.27
" "	M_4	1.73 *	1.18
" "	M_5	2.89 *	4.63**
" "	M_6	6.55 **	22.17**
Secondary branches	M_2	1.79**	1.59**
" "	M_3	1.94**	2.09**
" "	M_4	1.61*	1.81**
" "	M_5	2.21*	2.12**
" "	M_6	2.53**	0.05

* Significant at 5% level.

** Significant at 1% level.

Table 3
Performance of tetraploid Toria Selections
(M_6 generation) at different locations

Treatment	Location	Primary branches	Secondary branches	Number of seeds per siliqua
Control	Kanpur	8.3	5.5	10.7
Control	Bhubaneshwar	6.5	7.5	13.2
Control	Delhi	*	*	*
96 Kr	Kanpur	9.6	11.3* *	10.6
96 Kr	Bhubaneshwar	6.0	13.2**	14.5
96 Kr	Delhi	13.0	19.8	12.7
128Kr	Kanpur	9.3	9.9	9.5
128Kr	Bhubaneshwar	5.7	9.7	12.0
128Kr	Delhi	10.4	16.2	15.5

* Data obscured by poor plant growth caused by soil alkalinity

** Significantly superior.

a restricted genotypic spectrum. Cross-pollination in such instances is not synonymous for heterozygosity. This could be one factor responsible for the striking selection advance made in irradiated cultures, in contrast to the lack of response to selection met with in the control families. The improvement of autotetraploid toria for the number of secondary branches through induced polygenic variation is yet another example of the value of the mutation breeding technique for special purposes in plant breeding.

Acknowledgement: Our sincere thanks are due to Dr. B.R. Murty and Mr. V. Arunachalam for advice on statistical analysis and to Mr. A. Khan for help in recording and analysis of field data. We are also grateful to Messrs S.B.P. Rao and R.N. Mohanty for conducting the trials at Kanpur and Bhubaneswar respectively.

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Control	21	6.54	4.02 (9.29)*	9.24	14.93 (23.9)
X-ray, 96 Kr	78	6.48	3.86 (10.09)	9.24	26.47 (26.2)
X-ray, 128 Kr	72	6.38	3.28 (9.36)	8.77	23.95 (26.4)
	C.D.	0.26	1.48 (1.48)	0.84	5.0 (6.0)
<u>M_3 generation</u>					
Control	15	6.89	5.88 (11.53)	6.49	24.37 (25.3)
X-ray, 96 Kr	66	6.71	6.73 (13.65)	6.64	31.03 (25.1)
X-ray, 128 Kr	60	6.55	5.98 (12.14)	6.38	29.73 (24.9)
	C.D.	0.60	2.38 (2.38)	0.78	3.5 (3.52)

Standard error of the mean for calculating (C.D. was ~~taken~~ ^{computed} ~~calculated~~ by using harmonic means of number of observations in each treatment)

*: values in the brackets are averages of transformed variances ~~which are~~ and ~~which~~ the C.D. is ^{also} from the transformed data.