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Quantitative Studies on the Mating System of Jute *(Corchorus capsularis* L.)

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Summary. Nearly 35,000 individuals of *C. capsularis* were scored for selfing versus outcrossing in various populations. Different marker loci, such as anthocyanin pigmentation (C/c), serrated leaf (Sr/sr) and fasciated stem (Fs/fs), were used to determine the male gametes which had effected fertilization. The estimates of the outcrossing parameter, α, were found to differ with years, locations and for the marker locus used in the estimation. The outcrossing for C/c was lowest, the outcrossing for Fs/fs was highest and that for Sr/sr was intermediate. The nature of outcrossing, in general, was nonrandom. Selfing predominated in this species.

Introduction

The amount and nature of genetic variability in a population depend in part on its mating system. Mating systems vary between and within species. Many plant species have mating systems which allow partial intermating in addition to self-fertilization. Fyfe and Bailey (1951) and Nei and Syaktdo (1958) have given estimation procedures which assume no selection and population equilibria for gene frequencies. Allard and Workman (1963) and Harding and Tucker (1964) have given methods for estimating an outcrossing parameter when selection is present and/or equilibrium can not be assumed. These methods are based on estimates of gene frequency in the population and estimates of the frequency of dominant individuals appearing in the progeny of recessive individuals taken at random from the population.

Corchorus capsularis L., one of the commonly cultivated jute species, is mainly self-pollinated (Fryxell, 1957). The extent of natural cross-pollination in this species, using the anthocyanin locus as marker, was reported to be highly variable by Ghose and Dasgupta (1945) and Dutt and Ghose (1962). Whether cross-pollination is random or not has not been studied. The purpose of this investigation was to study in detail the mating system involved in certain artificial populations of this species using different loci, years and locations.

Materials and Methods

F_2 populations of different crosses between two varieties differing in dominant and recessive genes were used in this experiment. Outcrossing was estimated for three different loci: red-green anthocyanin pigmentation (C/c) without any consideration of its intensity and distribution; nonserrated - serrated leaf margin (Sr/sr); and nonfasciated - fasciated stem (Fs/fs). Outcrossing using the C/c locus was studied in Narendrapur in 1964 and in Haringhata in 1966 and 1971. Outcrossing rates using the Sr/sr and Fs/fs loci were estimated in the populations grown in Haringhata in 1971. The gene frequency, q, in each F_2 population was assumed to be approximately 0.5 and hence p or q was taken to be equal to 0.5 in calculations.

The estimation procedures developed by Harding and Tucker (1964) were followed. If a random sample of recessives is selected from a population, then a heterozygotes and b recessive homozygotes will be observed in their offspring. The observed proportion of outcross, $\hat{T}$, and its variance are:

$$\hat{T} = \frac{a}{a+b} \tag{1}$$

and

$$\mathrm{Var}\ \hat{T} = \frac{ab}{(a+b)^3} \tag{2}$$

which are the maximum likelihood estimators. However, not all crosses will be observed because homogeneous matings result in homozygotes. The maximum likehood estimate of total outcrossing, $\hat{\alpha}$, is

$$\hat{\alpha} = \frac{\hat{T}}{(1-q)} \tag{3}$$

where q is the gene frequency associated with the homozygote selected. If q is known, then using maximum likelihood method

$$\mathrm{Var}\ \hat{\alpha} = \frac{(1-\alpha p)}{Np} \tag{4}$$

where $p + q = 1$ and $N = a + b$.

The expected standard deviation (σ_α) and the observed standard deviation ($s\alpha$) of α were computed following Harding and Tucker (1964).

The same method of estimation of α was followed for the data published by Dutt and Ghose (1962). The authors studied cross-pollination in populations where homozygous dominant and homozygous recessive were equally frequent; hence q was taken to be 0.5 in the estimation of α.

Table 1. Estimates of outcrossing for different years and locations using the C/c locus as marker

Location/year	Cross	a*	N†	$\hat{\alpha}$	$\sigma_{\hat{\alpha}}$
Narendrapur, 1964	JRC 13 × Maniksari	87	5380	0.0323	0.0191
	JRC 212 × Maniksari	47	3470	0.0271	0.0238
	Total	134	8850	0.0303	0.0149
Haringhata, 1966	JRC 13 × Maniksari	24	1043	0.0460	0.0432
	JRC 212 × Maniksari	18	1725	0.0208	0.0338
	JRC 212 × Mogra	18	1284	0.0280	0.0392
	Total	60	4052	0.0296	0.0220
Haringhata, 1971	JRC 412 × TP	52	2809	0.0370	0.0264
	EC 4142 × TP	123	4449	0.0553	0.0651
	JRC 1 × TP	5	113	0.0885	0.1300
	JRC 321 × TP	43	1141	0.0754	0.0410
	D 154 × CNB	76	949	0.1602	0.0439
	Total	229	9481	0.0631	0.0142
	Grand Total	423	22383	0.0378	0.0093
Dutt and Ghose (1962) Barrackpore		175	20880	0.0168	0.0097

* Heterozygotes
† Total offspring

Results

Anthocyanin locus (C/c):

Table 1 presents the frequencies of heterozygotes, total F_3 offspring, estimates of outcrossing and their standard deviations for different crosses, years and locations. Binomial index χ^2's for the test of heterogeneity of the estimates of outcrossing revealed that the crosses within Narendrapur in 1964 ($\chi^2_{1df} = 91.20$; $P = < 0.001$) and within Haringhata in 1971 ($\chi^2_{4df} = 190.56$; $P = <0.001$) were heterogeneous, while the crosses within Haringhata in 1966 ($\chi^2_{2df} = 1.39$; $P = 0.50 - 0.30$) were homogeneous. Two crosses JRC 13 × Maniksari and JRC 212 × Maniksari in Narendrapur and Haringhata (1966) were similar and the individual pooled estimates of outcrossing in these two locations were compared and found to be homogeneous ($\chi^2_{1df} = 2.77$; $P = 0.20 - 0.10$). Binomial index chi squares did not indicate homogeneity for the estimates between years ($\chi^2_{2df} = 467.14$; $P = <0.001$), between locations of Narendrapur and Haringhata ($\chi^2_{1df} = 81.83$; $P = <0.001$) or between years within Haringhata location ($\chi^2_{1df} = 64.01$; $P = <0.001$). The lack of homogeneity, however, does not explain whether the differences in the estimates of outcrossing were due to variation in locations or years or both. Since the populations varied genetically, the entire variation can not be attributed to environment alone. However, all the observations over locations and years were pooled and a composite estimate was made, giving $\bar{\alpha} = 0.0378$. The observed fluctuation of this composite estimate (s_α) was more than twice ($s_\alpha/\sigma_\alpha = 2.15$) the expected random fluctuation (σ_α). The estimate of outcrossing from the data of Dutt and Ghose (1962) appeared to be much smaller than in the present observations. The heterogeneity test for the outcrossing estimates in Narendrapur, Haringhata and Barrackpore also revealed that they were different ($\chi^2_{2df} = 361.27$; $P = <0.001$).

Leaf serration locus (Sr/sr):

The frequencies of heterozygotes, total F_3 offspring, estimates of outcrossing and their standard deviations for Sr/sr locus are presented in Table 2. The binomial index chi square test revealed that outcrossing in different crosses was heterogeneous ($\chi^2_{5df} = 108.47$; $P = < 0.001$). The male parent, Tripura (TP), was common to all the crosses so the difference in outcrossing in these crosses may be attributed to the genotypic difference due to the female parents. All the observations for this locus were pooled and a composite estimate was made, giving $\bar{\alpha} = 0.0885$. The observed fluctuation

Table 2. Estimates of outcrossing using the Sr/sr locus as marker

Location/year	Cross	a*	N†	$\hat{\alpha}$	$\sigma_{\hat{\alpha}}$
Haringhata, 1971	CNB x TP	139	2760	0.1007	0.0262
	JRC 412 x TP	96	2265	0.0848	0.0290
	D 154 x TP	8	162	0.0988	0.1080
	EC 4142 x TP	184	5107	0.0721	0.0194
	JRC 1 x TP	36	834	0.0863	0.0479
	JRC 321 x TP	51	493	0.2069	0.0603
	Total	514	11621	0.0885	0.0128

* Heterozygotes
† Total offspring

Table 3. Estimates of outcrossing in different crosses using C/c and Sr/sr loci simultaneously, the female parent being c c sr sr

		a*		N†	$\hat{\alpha}$		$\sigma_{\hat{\alpha}}$	
Location/year	Cross	C/c	Sr/sr		C/c	Sr/sr	C/c	Sr/sr
Haringhata, 1971	JRC 412 x TP	11	12	296	0.0744	0.0810	0.0807	0.0806
	EC 4142 x TP	25	32	583	0.0856	0.1098	0.0573	0.0569
	JRC 1 x TP	3	8	66	0.0908	0.2424	0.1700	0.1631
	JRC 321 x TP	17	44	266	0.1276	0.3308	0.0838	0.0790
	Total	56	96	1211	0.0924	0.1584	0.0350	0.0357

* Heterozyhotes
† Total offspring

of the outcrossing was more than four times the fluctuation expected on the basis of chance alone ($s_\alpha/\sigma_\alpha = 4.31$), indicating the nonrandom nature of outcrossing. The rates of outcrossing scored independently using anthocyanin and leaf serration locus in F_2 populations of the crosses JRC 412 x TP, EC 4142 x TP, JRC1 x TP and JRC 321 x TP, in Haringhata in 1971 were compared. Binomial index chi square test showed that the outcrossing rates for these loci were heterogeneous ($\chi^2_{1df} = 5.48$; $P = <0.02$). In these crosses some F_2 progenies were doubly recessive for anthocyanin and leaf serration (i.e. c sr/c sr) loci. Outcrossing effected simultaneously for these loci by the corresponding dominant genes in that population were detected and considered for comparisons of outcrossing. Table 3 presents the simultaneous frequencies of heterozygotes for these loci, total F_3 offspring, outcrossing estimates and their standard deviations. It can be seen from this table that in all the crosses the estimates of outcrossing at leaf serration locus were consistently greater than those at anthocyanin locus. This indicates that the Sr is a more effective male parent in cross-pollination than the C parent since the females were the same. Mean estimates of outcrossing at these two loci over all the crosses were found to be heterogeneous ($\chi^2_{1df} = 24.02$; $P = <0.001$).

Fasciated stem locus (Fs/fs):

The frequencies of heterozygotes, total F_3 offspring, outcrossing estimates and their standard deviations are presented in Table 4. The binomial index chi square shows that crosses were heterogeneous ($\chi^2_{1df} = 5.89$; $P = < 0.02$) in their outcrossing estimates. The female parent, CNB, being common to both the crosses, the difference in outcrossing in the crosses was due to the differing male parents. As in the other loci, the observed fluctuation of mean estimates of outcrossing was greater than the fluctuation expected to occur randomly ($s_\alpha/\sigma_\alpha = 1.96$), indicating nonrandomness of outcrossing.

Comparisons showed that the amount of outcrossing using the Fs/fs locus was the highest and that using the anthocyanin locus C/c was the lowest. Estimated outcrossing rates at the three loci studied were heterogeneous ($\chi^2_{2df} = 149.16$; $P = <0.001$).

Table 4. Estimates of outcrossing using the Fs/fs locus as marker

Location/year	Cross	a*	N†	$\hat{\alpha}$	$\sigma_{\hat{\alpha}}$
Haringhata, 1971	CNB x TP	65	775	0.1677	0.0486
	CNB x D 154	10	184	0.1087	0.1013
	Total	75	954	0.1564	0.0439

* Heterozygotes
† Total offspring

Discussion

A study involving different loci, crosses, locations and years has shown that the amount of outcrossing was generally heterogeneous and nonrandom. There was, however, one exception: outcrossings involving an anthocyanin locus in three crosses within Haringhata in 1966 were homogeneous. Earlier studies in *Corchorus olitorius* L. involving different loci, locations, years and seasons showed that the amount of outcrossing was also heterogeneous and nonrandom (Basak and Chaudhuri 1966; Basak and Gupta 1972). In many other species, such as *Phaseolus lunatus* (Harding and Tucker 1964), *Phaseolus aureus* (Dana 1969), barley (Jain 1961) and maize (Gutierrez and Sprague 1959), outcrossing has also been found to be nonrandom.

In the present study, the comparisons between years or locations did not establish whether either one or both of them was responsible for the observed difference in outcrossing, since the contrasts were not orthogonal. But the differences among the crosses within a particular locus have indicated possible genotypic control of outcrossing. The results of comparisons of the crosses having common made on female parents confirmed this observation. The possibility of genotypic control was also evident from the wide variations of estimated outcrossing for different crosses with a common locus. From the present observations, however, the precise nature of genetic control could not be elucidated. The marker loci used in this study were found to have different rates of outcrossing. For instance, the Sr locus as male effected a higher rate of outcrossing than did the C locus. Harding and Tucker (1964) observed in *Phaseolus lunatus* that the estimates of outcrossing for the loci W/w, D/d, C/c and S/s were different.

The range of variation in estimates of outcrossing in the related species *C. olitorius*, involving different crosses and four loci, was between 0.0746 and 0.3030 (Basak and Gupta, 1972). The range of variation in the present study on *C. capsularis* was between 0.0208 and 0.2069. The nature of outcrossing being nonrandom in both species, the rate of outcrossing in *C. olitorius* is greater than that in *C. capsularis*.

The mating system is commonly considered to be one of the main factors determining the genetic structure and evolutionary potential in a population. The observed variability in the mating system of jute under the influence of genetic and environmental factors may well contribute to a complex population structure. The population structure in inbreeding species is much more complicated than commonly supposed and probably does not take the same form in all inbreeding species or even in different populations of the same species (Allard, Jain and Workman 1968).

The present evidence does not suggest that jute populations follow models of complete random mating or complete inbreeding, rather that the mating system of the present populations is partial inbreeding. Workman (1964) and Allard, Jain and Workman (1968) have discussed in detail the evolutionary consequences and significance of such a mating system.

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