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Analysis of Genetic Changes in Radiated and Non-radiated Bulk Oat (*Avena sativa* L.) Populations

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Summary. In both radiated and non-radiated oat populations inbreeding coefficients increased more slowly than was expected on the assumption of full selfing and equal selective values for homozygotes and heterozygotes. Assuming 1% outcrossing for oats and a selective value of 1.0 for the mean, the heterozygotes for two loci governing crown rust reaction have an advantage of 50% over the homozygotes. This study supports previous observations that the heterozygote often has a decided advantage in predominantly self-pollinated crops.

Key words: Selective values – Heterozygote advantage – Inbreeding coefficient – Mixed selfing – Maximum likelihood

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1 Introduction

A number of studies of populations of self-fertilizing plants have shown that many loci are heterozygous in such populations (Clegg et. al. 1978; for review see Allard et. al. 1968). In the present study changes in heterozygosity at two rustreaction loci were analysed in oat (*Avena sativa* L.) populations of radiated and non-radiated descent. The radiation treatment was applied to induce male sterility and led to increased outcrossing. The results obtained indicate that the heterozygotes at these loci had a decided selective advantage over the homozygotes.

2 Material and Methods

The materials of this study were a bulk oat population that was produced by compositing F_2 seeds from 250 crosses. After one increase of the bulk, the F_3 seed lot was subdivided into two lines of descent. The first line of descent (Pop. I) received no radiation treatment; seeds from the second line of descent (Pop. II) were radiated for four successive generations. The F_4 and F_5 were treated with thermal neutrons at total dosages of 1.3×10^{13} neutrons per cm ± 15% over an 8-hr period. Radiation treatment induces male sterility, the treated F_4 and F_5 seeds were consequently sown in alternating rows with the F_3, which served as a pollen donor. F_6 and F_7 seeds of Pop. II were treated with 20,000 r and 15,000 r of X-rays respectively, and the progeny of the F_5 of this population served as a pollen donor. No radiation treatment was applied after the F_7, and the population was propagated in bulk without selection through F_{11}.

Approximately 100,000 seeds were sown per generation in rows 2.5 m long and 30 m apart for both lines of descent. Seeding rate was one seed per cm of row. Plants were protected from foliage diseases by spraying them with the fungicide Zineb (Zinc ethylenebis-dithiocarbamate) at weekly intervals from anthesis to maturity.

3 Census Data

To estimate the proportions of the plants in Pops. I and II that were homozygous resistant, heterozygous, and homozygous susceptible to crown rust (*Puccinia coronata* cda. var. 'avenae' Fraser and Led), the reactions of progenies from individual plants from the two lines of descent to races 205 and 213 were determined. Reactions (susceptible or resistant) to these races are inherited monogenically. Seeds from 100 to 300 plants in each of several generations from each line of descent were sown in the greenhouse, and the resultant seedlings were tested for reaction to rust using the method described by Murphy (1935). Progenies were classified as homozygous resistant (P), heterozygous (R), and homozygous susceptible (Q) when disease symptoms had fully developed. The inbreeding coefficient F was calculated as $P/p + Q/q-1$ (Haldane and Moshinsky 1939), where p and q are the frequencies of the resistant and susceptible genes respectively.

4 Estimation of Selective Values

In a population where mixed selfing and random outcrossing operates, the recursions relating the frequencies of the

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three genotypes at a diallelic locus in generations n and n + 1, assuming selection, are:

$$\begin{aligned} &RR: f_1^{n+1} \propto w_1 \{S(f_1^n + 1/4 f_2^n) + t(f_1^n + 1/2 f_2^n)^2\} \\ &Rf: f_2^{n+1} \propto 1/2 S f_2^n + 2t(f_1^n + 1/2 f_2^n)(f_3^n + 1/2 f_2^n) \quad (1) \\ &rr: f_3^{n+1} \propto w_3 \{S(f_3^n + 1/4 f_2^n) + t(f_3^n + 1/2 f_2^n)^2\}, \end{aligned}$$

where f_i^n and f_i^{n+1} are the genotypic frequencies in generations n and n + 1 and w_1, w_3 are the selective values of RR and rr respectively. The selective value of the heterozygote Rr is set at equalling 1. The proportions of selfing and outcrossing are s and t respectively. The above recursions were first given by Hayman (1953) and solved for w_1 and w_3 by Allard and Workman (1962).

In this experiment, selective values were estimated assuming 20 levels of outcrossing for $0.001 \leq t \leq 0.01$ and $0.01 \leq t \leq 0.1$.

If (1) is written as

$$\begin{aligned} &f_1^{n+1} \propto w_1 k_1 \\ &f_2^{n+1} \propto w_2 k_2 \\ &f_3^{n+1} \propto w_3 k_3, \end{aligned}$$

and the observed proportions f_1, f_2, f_3 are denoted in generation n by P, R, Q and, in generations n + 1, by 0_1, 0_2, 0_3, then the maximum likelihood estimates are:

$$L \propto \{\frac{f_1^{n+1}}{\Sigma f_i n+1}\}^{0_1} \{\frac{f_2^{n+1}}{\Sigma f_i n+1}\}^{0_2} \{\frac{f_3^{n+1}}{\Sigma f_i n+1}\}^{0_3}$$

$$= E(0_1)^0 1\, E(0_2)^0 2\, E(0_3)^0 3$$

$$\ln L = \sum_{i=1}^{3} 0_i \ln E(0)_i = C. \quad (2)$$

The solutions for selective values w_1 and w_3 are

$$w_1 = \frac{0_1 \{1/2\, SR + 2\,t\,(P + 1/2\,R)(Q + 1/2\,R)\}}{0_2\, S(P + 1/4\,R) + t(P + 1/2\,R)^2}$$

$$w_3 = \frac{0_3 \{1/2\, SR + 2\,t\,(P + 1/2\,R)(Q + 1/2\,R)\}}{0_2\, S(Q + 1/4\,R) + t(Q + 1/2\,R)^2}\,.$$

The variances of the estimates of w_1 and w_3 are respectively,

$$(1-0_3)(0_3 - K_2^2)/0_2^3\, K_1^2\, N$$

ard $(1-0_1)(0_3 K_2^2)/0_2^3\, K_2^2\, N$,

Where N is the total sample size in generation n + 1. Allard and Workman (1962) also defined the effective amount of outcrossing as:

$$f_2^n - 2f_2^{n+1} / 4\{-f_1^n f_3^n + 1/4\,(f_2^n)^2 - 1/4\, f_2^{(n)}\}.$$

5 Results and Discussion

Although the samples used for each generation were small, the standard error of the estimated gene frequency, p, was <0.04 for the two races in every instance. In both lines of descent, the estimated inbreeding coefficients rose less rapidly than expected assuming full selfing (Tables 1, 2). Imam and Allard (1965) reported that outcrossing in wild oats (*A. fatua* L.) in California varied from 1% to 12% and

Table 1. Proportions of homozygous resistant (P), heterozygous (R), and homozygous susceptible (Q), gene frequencies (p & q), and expected and estimated inbreeding coefficients for the locus in the oat genome that differentiates reactions to race 205 of crown rust, and the estimated percentage of outcrossing in Pops I and II of oats

Generation	Genotypic frequencies			Number plants sampled	Gene frequencies		Inbreeding coefficients		Percent outcrossing
	P	R	Q		p	q	Expected	Estimated	
Pop I									
F_3	0.61	0.14	0.25	234	0.68	0.32	0.50	0.68	0.07
F_4	0.64	0.09	0.27	225	0.68	0.32	0.75	0.78	–
F_5	0.62	0.10	0.28	156	0.67	0.33	0.88	0.77	–
F_8	0.70	0.04	0.26	274	0.72	0.28	0.98	0.89	0.01
F_9	0.79	0.03	0.18	191	0.80	0.20	0.99	0.92	0.03
F_{10}	0.72	0.02	0.26	247	0.73	0.27	1.00	0.94	–
Pop II									
F_4	0.64	0.12	0.24	180	0.71	0.29	0.75	0.71	–
F_5	0.62	0.13	0.25	141	0.68	0.32	0.88	0.69	–
F_9	0.65	0.07	0.28	207	0.68	0.32	0.99	0.83	0.05
F_{10}	0.67	0.06	0.27	178	0.70	0.80	1.00	0.87	0.04
F_{11}	0.71	0.04	0.25	133	0.73	0.27	1.00	0.89	–

Table 2. Proportions of homozygous resistant (P), heterozygous (R), and homozygous susceptible (Q), gene frequencies (p & q), and expected and estimated inbreeding coefficients for the locus in the oat genome that differentiates reactions to race 213 of crown rust, and the estimated percentage of outcrossing in Pops I and II of oats

Generation	Genotypic frequencies			Number plants sampled	Gene frequencies		Inbreeding coefficients		Percent outcrossing
	P	R	Q		p	q	Expected	Estimated	
Pop I									
F_3	0.72	0.11	0.17	298	0.77	0.23	0.50	0.68	–
F_4	0.68	0.14	0.18	226	0.75	0.25	0.75	0.62	–
F_8	0.81	0.03	0.16	182	0.32	0.18	0.98	0.90	0.05
F_9	0.84	0.03	0.13	184	0.85	0.15	0.99	0.89	0.05
F_{10}	0.85	0.02	0.13	286	0.86	0.14	1.00	0.91	–
Pop II									
F_4	0.71	0.11	0.18	282	0.72	0.24	0.75	0.71	–
F_9	0.73	0.05	0.22	185	0.73	0.27	0.99	0.77	0.04
F_{10}	0.75	0.04	0.21	217	0.77	0.23	1.00	0.90	0.01
F_{11}	0.71	0.02	0.27	260	0.72	0.28	1.00	0.96	–

that percentage outcrossing varied with the character investigated, and the population. Grindeland and Frohberg (1966) reported outcrossing between 0.3 and 2.0% in untreated oats, whereas in radiated oat populations, outcrossing of 4.1% to 5.9% was observed. They concluded that thermal-neutron treatment increased outcrossing by a factor of 6. Inbreeding coefficients and percentage outcrossing (assuming equal fitness values for the three genotypes) are indirect measures of outcrossing in Pops. I and II. These two measures gave no evidence that radiation (Pop. II) promoted outcrossing in progenies of radiated seeds. Outcrossing percentages for both populations were low and similar.

Table 3. Selective values for homozygous resistance (RR) and homozygous susceptible (rr) genotypes for reactions to races 205 and 213 of crown rust in Pops I and II, assuming 1.0 and 2.0 percent outcrossing

Generation	Genotype	Pop I				Pop II			
		Race 205		Race 213		Race 205		Race 213	
		1.0%	2.0%	1.0%	2.0%	1.0%	2.0%	1.0%	2.0%
F_3	RR	–	–	0.39	0.41	–	–	–	–
	rr	–	–	0.38	0.40	–	–	–	–
F_4	RR	0.76	0.89	–	–	–	–	–	–
	rr	0.74	0.79	–	–	–	–	–	–
F_5	RR	0.46	0.50	–	–	0.44	0.47	–	–
	rr	0.48	0.51	–	–	0.46	0.48	–	–
F_8	RR	–	–	0.63	0.73	–	–	–	–
	rr	–	–	0.49	0.57	–	–	–	–
F_9	RR	1.11	1.28	0.77	0.88	–	–	0.79	0.89
	rr	0.66	0.77	0.72	0.83	–	–	0.69	0.77
F_{10}	RR	0.60	0.71	–	–	0.71	0.79	–	–
	rr	0.91	1.10	–	–	0.67	0.74	–	–
F_{11}	RR	–	–	–	–	0.73	0.82	–	–
	rr	–	–	–	–	0.62	0.71	–	–
Mean	RR	0.73	0.82	0.60	0.67	0.63	0.69	0.79	0.83
	rr	0.70	0.79	0.53	0.60	0.58	0.64	0.69	0.77

Reported studies on outcrossing by Grindeland and Frohberg (1966), in oats, have shown that outcrossing varied from year to year. The indirect measures in this study also indicate that outcrossing varied from year to year.

Because studies of cultivated oats in Iowa indicate that outcrossing is usually less than 2.0%, we computed the selective values for the homozygous resistant and homozygous suspectible plants (Table 3) on the assumption of 1.0 and 2.0% outcrossing. Assuming an outcrossing level of 1.0% in oats, and a selective value of 1.0 for the mean, selective values of the homozygous resistant and homozygous susceptible plants for races 205 and 213 ranged from 0.60 to 0.79 and 0.53 to 0.70, respectively, and their overall weighted means were 0.67 and 0.62, respectively. Thus, the heterozygotes have an advantage of ca. 50% over both homozygotes. The homozygous resistant genotype had a slight advantage in selective value, but the difference between 0.67 and 0.62 probably is of little significance. There is no evidence that the frequency of the resistant gene (p) had increased in either Pop. I or Pop. II (Tables 1, 2).

One consequence of heterozygote advantage of this magnitude is that such loci will remain polymorphic (Hayman 1953). Jain and Allard (1960), Allard et al. (1972) and Weir et al. (1974) found that the proportion n of heterozygotes at a number of marker loci in barley populations did not decrease at the expected rate under the observed levels of selfing and outcrossing. They concluded that the adoption of inbreeding is not necessarily accompanied by the relinquishment of heterozygote advantage. Thus, the storage of variability in self pollinated plants is not entirely dependent on genetic diversity among multiple homozygous familial lines but is also dependent on heterozygote advantage.

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