THE BREEDING SYSTEM OF *CHENOPODIUM QUINOA*

I. MALE STERILITY

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1. INTRODUCTION

Chenopodium quinoa is a minor economic plant of the high Andes (review in Simmonds, 1965). Under various names, of which quinoa is the most widely used, it is grown for its grain which is made into porridge, flour and beer. It is commonest at high altitudes (up to about 4,000 metres) in Peru and Bolivia and overlaps maize cultivation at the lower levels down to about 2,000 metres. It is, in effect, a primitive cereal and has been selected, as have the cereal grasses, for large grains, non-shattering inflorescences and low seed dormancy. It may be thought of as the New World analogue of buckwheat, *Fagopyrum*. The species is tetraploid with $2n = 36$ chromosomes. Hermaphrodite plants bear abundant good pollen and the genetical evidence adduced below suggests that it is an amphidiploid showing disomic inheritance.

The study reported here arose from the finding that one seed sample out of several collected in Peru and Bolivia in 1963 yielded female as well as hermaphrodite plants; that is, the population was gynodioecious. Genetical analysis of this character, as will be shown, has yielded some rather curious results. Population aspects will be treated in a later paper.

2. MATERIALS AND METHODS

Two stocks were used in the studies reported here. One, the more important and the only recorded source of gynodioecy in the species, was acquired in 1963 as a packet of seed* in the market at Batallas on the altiplano of Bolivia near La Paz. In Britain, it is of medium maturity, not so late as some other stocks but not so early as the other strain referred to here: this was a botanic garden stock of remarkably uniform appearance and early maturity (perhaps reflecting a history of inbreeding and selection) acquired from the Brussels Botanic Garden in 1964. The Brussels stock ripens seed easily in Britain; the Batallas stock also does well in the south of England but is marginally adapted to Scotland; several other stocks are much later and cannot be successfully grown outdoors at all. Plants of all stocks are extremely plastic, ranging from one to two metres tall in the field down to several centimetres when crowded in pots or boxes in the glasshouse. About 30 plants can be grown to maturity per 15 cm. pot so, for experimental purposes, the species can be quite economical of space. In the field, sowing in rows 60-100 cm. apart, followed by thinning to a spacing of 15-30 cm. between plants in the rows has proved satisfactory.

* Conveniently "seed" but strictly fruit since the propagules are achenes with thin, tough, adherent pericarps.

Pollen is windborne and seed-setting in the field in dry sunny weather is good. In the glasshouse, pollination is much less effective and females set at best only about half as many seeds as hermaphrodites. Unfortunately, controlled pollinations are very difficult; flowers are extremely small and the inflorescences are more or less leafy. Setting of seed inside any kind of a closed bag is bad since the whole or nearly the whole plant has to be enclosed. Isolation of single plants or pairs of plants (female and hermaphrodite) in separated glasshouses has given good results. Female by hermaphrodite crosses can also be got by growing parents in a single pot which is covered at maturity in a polythene sleeve supported on canes, open at the top and much taller than the plants; plants will set seed under these conditions and the risk of contamination is greatly reduced (though not eliminated). Hermaphrodites in the glasshouse are fairly highly self-pollinated and, for most test purposes, open-pollinated progenies suffice.

3. RESULTS

(i) *The loci R, Ax and Ms*

The following results all refer to the Batallas stock. The locus *R* controls pigment (betacyanin) production in the upper stem and inflorescence. In the stock as a whole, pigmentation is extremely variable. Within- and between-family variation suggests an allelic series of dominant *R*; the recessive *rr* lacks pigment. Classification for pigment/no pigment is easy except under low light intensities and at the lowest levels of genetical expression of *R*, when occasional *R* plants may be misclassified *rr*. Many families bred true for red or green; 38 segregating families gave 1002 *R*: 321 *rr* ($\chi^2[1] = 0.38$).

The locus *Ax* controls the production of an axillary pigment spot which, like *R*, varies in intensity in different families. The recessive (*axax*) lacks the spot; classification is good except in families carrying a strong *R*, when it may be impossible. Many families bred true for spot or no spot; 31 families segregated 824 *Ax* : 269 *axax* ($\chi^2[1] = 0.09$).

The locus *Ms* affects anther development. Nearly all quinoas are gynomonoeious (*MsMs*); they bear mixtures of female and hermaphrodite flowers and the plants are functionally hermaphrodite (hereafter abbreviated *hh*). In *msms* plants the anthers are abortive (rudiments can be found) and the plants are functionally female (abbreviated *ff*). *MsMs* plants bred true; 101 heterozygotes yielded 2017 *Ms*: 691 *msms* ($\chi^2[1] = 0.448$) (table 5). Forty-two progeny tests of 11 true breeding families yielded only hermaphrodites; 130 progeny tests of hermaphrodites from 45 segregating families showed that 89 were *Msms* while 38 were *MsMs*, in good agreement with the expected 2 : 1 ratio ($\chi^2[1] = 0.665$) (table 4); there were, in addition, three anomalous families which will be referred to again (table 4). Male sterility, therefore, on the evidence of breeding from hermaphrodites, is determined by a simple recessive. Breeding results from females, described below, show that the situation is, in fact, much more complex than this.

Joint segregation data (table 1) shows that all three loci are linked:

$$Ax \text{---} 8\% \text{---} R \text{---} 35\% \text{---} Ms$$

but that *Ax* and *Ms* are nearly 50 units apart. The data of table 1 were assembled from observations of selfed hermaphrodites that were pheno-

typically *R*, *Ax* or *RAx*. Thus they are in effect F_3 data, and linkage phase was determined by inspection. This is admittedly an unsatisfactory procedure when linkage is weak, but the results appear to be unambiguous.

TABLE 1
Joint segregations in quinoa

Loci (A-B)	Families	Progeny				Linkage χ^2	p $\pm$ se.
		AB	Ab	aB	ab		
<i>Ms-Ax</i>	23	492	149	165	56	—	—
<i>R-Ax</i>	11	202	95	81	1	29.16 (R)	11.3 ± 5.1 (7.8 ± 1.9)
<i>R-Ax</i>	5	122	8	28	23	29.98 (C)	7.3 ± 2.0
<i>Ms-R</i>	7	146	55	50	4	7.68 (R)	29.2 ± 5.7 (34.5 ± 2.6)
<i>Ms-R</i>	11	273	60	66	41	17.60 (C)	36.0 ± 3.0

Note.—*Ms-Ax* data in the top line gave no evidence of linkage. In the last column, bracketed values are joint estimates from weighted means of coupling and repulsion values.

(ii) *The progeny of females*

Females do not breed as expected on the basis of a simple recessive male sterility. The evidence for this comes, first, from the progeny of females of unknown genetic history drawn from the general Batallas population (table 2) and, second, from experimental pollinations of females known from

TABLE 2
Progeny of open-pollinated female quinoas drawn from the Batallas population

Source	Families	Herm. (hh)	Female (ff)	hh per cent.	Range per cent.
Glasshouse	40	164	628	20.8	0.72
1964 field	25	2381	6572	26.6	14.45
1965 field	23	135	663	16.9	0.36
1968 field	33	169	405	29.4	0.55
Totals	121	2849	8268	25.6	0.72

Note.—The three field populations were raised from three subsamples of the original batch of South American seed, the first two at the John Innes Institute, the third at Pentlandfield.

breeding history to be *msms*. The first line of evidence is summarised in table 2. Breeding tests of the hermaphrodite pollinators in the same plots showed that most (about 88 per cent.) of the pollen was *Ms* so the generally high frequency of female progeny from female parents is incompatible with recessive male sterility. The proportion of females is quite variable and there was no indication of discrete frequency classes:

Percentages of families having stated percentages of hermaphrodites

0	1-10	20	30	40	50	60	70	80
7	24	20	26	13	5	5	0	1

A set of 23 glasshouse crosses of related females by *MsMs* plants yielded even more striking results: 512 progeny were all female. Collectively these results suggest a rather variably expressed cytoplasmic control of male sterility. On these data most females bear between 50 and 100 per cent. female progeny but no special significance attaches to these figures because it will be shown below that the range is much wider than this and there is, in any case, a significant environmental influence on the expression of male sterility.

TABLE 3
Progeny of female (msms) quinoas crossed by various hermaphrodites

Cross ff(<i>msms</i>) ×	Families	Plants	hh per cent.	
			Mean	Range
1. <i>MsMs</i>	37	1078	5	0-45
2. <i>MsMs</i>	16	513	13	0-48
3. <i>MsMs</i>	10	309	90	74-96
Subtotals	63	1900	21	0-96
4. <i>MsMs</i> +2 <i>Msms</i>	11	325	54	36-92
5. <i>MsMs</i> +2 <i>Msms</i>	46	1380	60	27-97
Subtotals	57	1705	59	27-97
6. <i>Msms</i>	31	844	40	13-81
7. <i>Msms</i>	20	545	58	38-88
Subtotals	51	1389	47	13-88

Notes.—

1. Mendelian expectations for lines 1-3, 100 per cent. hh; for lines 4-5, 67 per cent. hh; for lines 6-7, 50 per cent. hh.

2. In lines 4 and 5 random pollination of ff within segregating families, hh shown to occur in expected ratio 1 *MsMs*: 2 *Msms* (table 4).

3. In lines 1, 2, 3 and 7, hh parents were progeny-tested.

4. In line 6, hh parents were from ff parents and found by progeny test to be predominantly *Msms* (table 4 and text).

The second line of evidence comes from crosses of *msms* females derived from selfs of heterozygous hermaphrodites (table 3). At flowering, hermaphrodite siblings were removed and the surviving females were isolated with known *MsMs* pollinators or with hermaphrodites presumed to be *Msms*; alternatively, whole segregating families were isolated, in which case the pollen population would have been 67 per cent. *Ms*; alternatively, again, all but one hermaphrodite was removed as flowering began and the constitution of that plant later determined by progeny test. By these means *msms* females were pollinated by pollen known to be 50, 67 and 100 per cent. *Ms*.

The results of table 3 show that *msms* females produced a very wide range of frequencies of hh in their progeny and that the general run of frequencies is higher than in the open pollinated families summarised in table 2. *Ms* pollen alone produced nearly the entire range of observed frequencies of hh and it does not look as though the constitution of the pollen markedly affected hh frequency. That the pollen does have some effect, however, is shown by comparison of lines 3 and 7 of table 3. These data are based on pollinations of ff plants out of selfed heterozygotes by sibling hh pollinators

which were later progeny tested. Two lots of pollinations were done on the same families in 1968 and 1969, and the progenies were tested in 1969 and 1970. The results were (perhaps surprisingly) homogeneous for families and years but there was a significant effect of pollinator, thus:

Cross	het. χ^2	Families	hh	ff	hh %
<i>msms</i> $\times$ <i>Msms</i>	25.1 [19]	20	317	228	58
<i>msms</i> $\times$ <i>MsMs</i>	4.7 [9]	10	278	31	90

Homozygous male parents produced more hh progeny than heterozygous ones, though other items in table 3 show that this effect is only detectable when comparisons are made on a common genetic background.

The families represented by line 1 of table 3 contained ff all of nuclear constitution *Msms*. These were pollinated by hh *MsMs* and large numbers of females again appeared in the progeny, as follows: 17 families, totalling 586 plants contained 247 hh (42 per cent., family range 0-100 per cent.). Presumably half the 58 per cent. of ff plants in these families were of constitution *MsMs* and the constitution of the hh segregants in their progeny should provide evidence of this.

Collectively, these results again suggest the operation of an erratic cytoplasmic mechanism, but there is one fact that is hard to reconcile with this

TABLE 4
Constitution of hh plants of quinoa from two sources (cf. table 5)

Source	Families	Diagnosis			χ^2
		<i>MsMs</i>	<i>Msms</i>	pseudo-hh	
<i>Msms</i> selfed	130	38	89	3	0.665[1] for 1 : 2 ratio
per cent.	—	29.2	68.5	2.3	
hh ex ff	98	3	75	20	—
per cent.	—	3.1	76.5	20.4	—

idea. Lines 4-7 of table 3 all show that, contrary to the general expectation (on a cytoplasmic basis) of an excess of females, some families showed excesses of hermaphrodites when compared even with the simple Mendelian situation. Interpretation of this observation must await progeny tests of hermaphrodite segregants (which are yet incomplete). Meanwhile, it is clear from lines 1-3 of table 3 that plants of nuclear constitution *Msms* can be of female phenotype if bred from female parents, so some element of cytoplasmic control appears certain.

Cytoplasmic control of male sterility is also indicated by a back-crossing programme that was undertaken with the aim of producing an earlier maturing population better adapted for experimental purposes than the Batallas population. The starting materials were the progeny of a female carrying *R* and *Ax* and the early-maturing true-breeding Brussels stock (*rax Ms*); the maternal family had 20 per cent. hermaphrodites (which were discarded) and the F_1 and first two back-crosses to the Brussels stock were made as bulk crosses; these three generations had, respectively, 10, 7 and 4 per cent. hermaphrodites, so a persistent and fairly well expressed cytoplasmic control of male sterility is indicated. Evidently, the Brussels nucleus favours the expression of male-sterility.

It was shown above that hh plants bred from hh parents conform in constitution and breeding behaviour with Mendelian expectation: the data of tables 4 and 5 show that hh plants from ff parents, by contrast, behave rather differently. First, the majority (77 per cent.) of such hh plants turn out to be heterozygotes, *Msms*, or at least to produce selfed progeny in good agreement both with the Mendelian ratio and with the progeny of *Msms* plants bred from hermaphrodites (table 5). Homozygotes (*MsMs*) occur but are rare and there is a sizeable minority of plants that produce about 50 per cent. hh progeny; these are tentatively interpreted as weakly expressed females and called, for want of a better term, pseudo-hh. Such pseudo-hh plants occur in low frequency in the offspring of *Msms* plants; they might be

TABLE 5
Breeding tests of hh plants of quinoa from two sources (cf. table 4)

Parents	Families	Progeny		χ^2	
		hh	ff		
1. <i>Msms</i> from <i>Msms</i>	101	2017	691	0.448	[1] homogeneous
2. <i>Msms</i> from ff	75	1866	643	0.527	[1] homogeneous
Totals, 1 + 2	186	3883	1334	0.905	[1] homogeneous
3. Pseudo-hh from <i>Msms</i> per cent.	3 —	25 50.0	25 50.0	0.514	[1] (contingency)
4. Pseudo-hh from ff per cent.	15 —	215 44.7	266 55.3		

expected to produce a bias towards an excess of hh in test progenies but this is not evidently so, since the overall ratio from selfed heterozygotes (table 5) is 3883 hh : 1334 ff or 74.4 : 25.6. It will be noted that pseudo-hh plants from the two sources agree in producing about 50 per cent. hh progeny, a ratio and an agreement which may or may not be significant (but are most probably fortuitous).

The ff parents that yielded the results given in tables 4 and 5 were all either members of the original Batallas population or were a generation descended from it. They were open-pollinated by pollen that must have been predominantly *Ms* so the high frequency of heterozygotes (*Msms*) among their hh progeny implies a high frequency of the recessive allele, *ms*, among functional female ovules. Interpretation of this conclusion is not yet possible.

(iii) *An environmental effect*

It has been shown above (tables 2 and 3) that the frequencies of hh plants in the progeny of ff parents is widely variable (with an extreme range of 0 to 97 per cent.) and that this variability bears little relationship to the constitution of the *Ms* locus (since *Msms* families from female parents are from 0 to 94 per cent. hh). In the expectation that male sterility in quinoa (like cytoplasmically determined characters in general) might be susceptible to environmental influences, an experiment to test the effect of duplicate sowings at different times was set up.

Several hundred families from female parents were grown and scored during the spring and early summer of 1969 in a glasshouse at Pentlandsfield.

From these, 22 families were selected to cover a wide range of hh frequencies; remnant seed was sown in the summer of 1969 and scored in the early autumn; the plants were grown in the same glasshouse as the first lot and treated similarly, one family of average-size 30 plants being raised in a 15 cm. pot. The main environmental difference between the two lots was therefore time of year. Results (table 6) show that there was a significant and rather consistent environmental effect: families with low hh frequencies were low on both occasions but families with higher hh frequencies differed, the second

TABLE 6
Sex ratio in quinoa: variability with different occasions of sowing

hh frequency	Families tested		First sowing	Second sowing
Low (< 10%)	10	{ numbers	362	251
		{ hh per cent.	1.9	1.2
		{ range	0.13	0.11
High (> 10%)	12	{ numbers	385	368
		{ hh per cent.	32.2	49.4
		{ range	13.57	20.92
Totals	22	{ numbers	747	619
		{ hh per cent.	18.5	27.7
		{ range	0.57	0.92

sowing having many more hh plants than the first. Of the latter, all 12 individual comparisons favoured the late sowing and analysis of variance of angles gave:

	d.f.	V	VR	P
Times	1	679	17.1	Small
Families	11	159	4.0	1.5 %
T × F	11	40	—	—

The theoretical variance for a family of size 30 is 27, so the interaction variance, $T \times F$, is not large.

The conclusion is that the expression of male sterility in the progeny of female quinoas varies with growing conditions and that, therefore (as remarked above), no detailed interpretation of hh frequency data is possible. It is not yet known whether conditions at the time of pollination and seed development also affect hh frequency; comparison of tables 2 and 3 indeed suggests that glasshouse pollinations tend (sometimes) to produce higher frequencies of hh from ff parents than do field pollinations.

From this result it might perhaps be predicted that sex expression would vary also within the life of an individual plant. This is so, but the behaviour seems to be rare. In the progeny of ff plants, several instances of individuals scored as ff that later bore a hh branch (and *vice versa*) have been noted; but the great majority of the many plants that have been scored repeatedly have been consistently one or the other.

It should be emphasised that these results apply only to the progeny of ff parents, that is to the cytoplasmic phase of control of male sterility. A con-

siderable body of experience (acquired over seven seasons of work) goes to show that hh plants breed in a consistent Mendelian fashion (tables 1, 4 and 5); perhaps pseudo-hh plants will prove to be an exception to this rule.

(iv) *A grafting experiment*

Graft transmission of cytoplasmic male sterility has been reported several times, the best documented case being that of *Petunia* (Frankel, 1956; Edwardson and Corbett, 1961; but see also van Marrewijk, 1970). An experiment with quinoa has given negative results. The materials used were remnant seed of progeny of ff known to have high ff frequencies and several

TABLE 7
A grafting experiment with quinoa

Material	Families	Plants	hh per cent.		Notes
			Mean	Range	
1. Cleft grafts					
hh on ff	6	230	100	—	—
ff on hh	3	93	15	7-19	—
2. Approach grafts					
hh	9	437	98	87-100	1
ff	10	394	40	0-100	—
3. Controls					
hh	10	363	98	81-100	2
ff	10	357	15	0-57	—

Notes—

1. ff occurred in two families out of nine in frequencies 1/62 and 6/46.
2. ff occurred in two families out of ten in frequencies 1/33 and 8/41.

hh lines known to have bred true for at least two generations. Plants were grafted as seedlings at about the five-leaf stage. Both cleft and approach grafts were made; for the former, hh scions were self-pollinated in isolation and ff scions crossed by hh controls; for the latter, the grafted pairs were isolated so that the hh components were selfed and the ff components crossed by the sister hh. There was no visible effect of grafting on sex expression in the grafted plants themselves. The progeny (table 7) gave no evidence of graft transmission, though it should be noted that the frequency of hh progeny from the ff parents tested was so variable that any but a very large and consistent graft effect would be very hard to prove.

A curious feature of the results is the occurrence of a few ff in three supposedly true-breeding hh control lines. One of these lines had bred true for three generations and had had no female parent in its recorded pedigree; the other two had bred true for two generations and had had a female parent four generations back. All these materials also bred true for *r* and *ax* and were reasonably uniform in facies so contamination by mixture or crossing is unlikely as an explanation of the appearance of ff progeny; the implication is that cytoplasmic determinants of male-sterility can be carried unexpressed (perhaps at a sub-threshold frequency within the cell) for several generations.

4. DISCUSSION

The genetic control of gynodioecy in quinoa is clear enough in outline though unresolved in detail: a recessive male sterility becomes a maternally transmitted cytoplasmic male sterility. Formally, the idea that the recessive *msms* nucleus generates a cytoplasmic anther suppressor meets the main facts. That there is indeed a nuclear determinant is shown by orderly Mendelian behaviour and by the happy accident of linkage to *R*. The cytoplasmic determinant is inefficient in the sense that females commonly produce at least some, and often many, hermaphrodite progeny. This uncertainty of expression (or transmission) is, of course, rather characteristic of cytoplasmically determined characters, as is also the element of environmental control revealed by the experiment on duplicate sowing. Two (probably important) facts which are yet uninterpretable on this basis are the production by some females of excessive numbers of hermaphrodites (where excess females would be predicted) and the finding that a majority of hermaphrodites produced by females are heterozygotes (*Msms*).

However these discrepancies may be resolved, there is, on the broad interpretation, an obvious similarity between this situation and the behaviour of three plastid mutants in other plants, namely: maize (iojap, Rhoades 1943, 1950); barley (Imai, 1936) and *Nepeta* (gene *m*, Woods and Du Buy, 1951). In all four cases, a recessive gene, when homozygous, generates a maternally transmitted non-nuclear defect. As in quinoa, the cytoplasmic determinants of the three plastid mutants were inefficient in the sense that maternal transmission was incomplete. Thus an iojap maize plant may produce white, variegated and green progeny, reflecting heterogeneity of distribution of the determinants within and between cells. In quinoa a similar heterogeneity may be inferred but is not so readily proved; the isolation of 100 per cent. female-transmitting lines would be evidence.

Transference of genetic control from nucleus to cytoplasm is paralleled not only by the plastid mutants mentioned above but also by the transition from the integrated to the autonomous phase of an episome. It was with this analogy in mind that the unsuccessful grafting experiment described in this paper was undertaken. If the analogy is to be taken further it will be necessary to show not only that there is an infective aspect but that nuclear reintegration of the cytoplasmic determinant takes place.

The cytoplasmic interpretation favoured so far in this paper has the merit of suggesting further experimentation and of drawing comparisons with the mutable plastid studies referred to above; it therefore has a certain heuristic value. However, this interpretation is by no means securely established and one other, seemingly somewhat contrasted, approach deserves mention, namely the possibility of some paramutation-like process. Formally, one could think of a genotypically controlled mass-mutation of *Ms* to *ms* as being responsible for the maternal pattern of inheritance of femaleness. At present there appears to be no means of choosing between the two interpretations; though contrasted in principle, they lead to similar results and it may be that quinoa will prove to be technically unsuitable for making a critical choice. If and until critical evidence becomes available, the cytoplasmic interpretation seems to be the better because less speculative.

Male sterilities have been recorded in some 60 species of flowering plants (review by Jain, 1959); the majority (about 80 per cent.) are due to recessive

nuclear genes, minorities to cytoplasm only and to cytoplasm interacting with nuclear genes. Obviously, however, these are categories of experimental convenience liable to change as work progresses. One might surmise that the great majority of male sterilities would turn out to be gene-plus-cytoplasm situations if thoroughly investigated. The quinoa system at present appears to be unique in that the cytoplasmic determination, once generated, overrides nuclear control; it differs in this from the normal cytoplasm and restorer system that is currently finding numerous uses in plant breeding. However, the quinoa system might be commoner than it seems to be; loss of *ms* from a population would leave simply a rather inefficient cytoplasmic system.

5. SUMMARY

1. *Chenopodium quinoa*, quinoa, is a minor grain-crop plant of the high Andes. Genetic studies of three loci are reported: *R* (red plant) *r* (green plant); *Ax* (axil spot) *ax* (none); *Ms* (hermaphrodite) *ms* (male-sterile). The three loci are linked thus: *Ax*—8%—*R*—35%—*Ms*.

2. Plants of genotype *MsMs* and *Msms* breed as expected; the recessive male-sterile, *msms*, breeds as though it carries an erratically expressed or transmitted cytoplasmic factor for male sterility.

3. There is some environmental variation in expression of male sterility. An experiment gave no evidence of graft-transmission of male sterility.

4. The results are taken to indicate that the recessive nucleus *msms* generates a cytoplasmic male-sterility factor and comparisons are drawn with *iojap* of maize and the gene *m* in *Nepeta*.

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Note added in proof.—A recent paper by D. Stroup (*J. Hered.*, 61, 139-141, 1970) adds yet another example to the list of cytoplasmic factors seemingly generated by recessive nuclear genes. This mutant (*cm*) in maize behaves rather like *iojap*.

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