

SEX DETERMINATION IN *POTENTILLA FRUTICOSA*

M. S. GREWAL and J. R. ELLIS

Department of Botany and Microbiology, University College, London, W.C. 1

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1. INTRODUCTION

Potentilla fruticosa L. sensu lato is a variable taxon cytologically with cytotypes forming a polyploid series from diploids with $2n = 14$, through tetraploids and hexaploids with $2n = 28$ and 42 respectively to octoploids with $2n = 56$ (Bowden, 1957). As far as is known the diploids are hermaphrodite, the tetraploids are either hermaphrodite or dioecious, and the higher polyploids ($6x$ and $8x$) are dioecious. The Linnaean type species *P. fruticosa* L. sensu stricto from Northern Europe is tetraploid and strictly dioecious (Tornblom, 1911). In the distribution of the hermaphrodite and dioecious forms *P. fruticosa* closely resembles the genus *Fragaria* which likewise has dioecy restricted to the polyploid species, while all the diploid species are hermaphrodites (Staudt, 1967).

In the angiosperms, the dioecious species of *Fragaria* are unique in having female heterogamety (Kihara, 1930; Staudt, 1952, 1955, 1967*a, b*, 1968; Westergaard, 1958), and it would be very desirable to establish whether a similar system of sex determination exists in the dioecious types of *Potentilla fruticosa*. Cytologically the chromosomes of *P. fruticosa* are too small to establish the heterogametic sex from observations of heteromorphy in either somatic or meiotic cells. Of the additional procedures listed by Westergaard (1958) and Burnham (1962) for establishing the heterogametic sex in dioecious angiosperms, one is applicable to the tetraploid cytotypes of *P. fruticosa*. This involves the analysis of the progenies from reciprocal crosses between dioecious and hermaphrodite types. If dioecism is dominant to hermaphroditism as in the closely allied genus *Fragaria* (Staudt, 1967), then the progeny from the heterogametic sex should segregate for both sex types, whereas the progeny from the homogametic sex should be uniform in sex expression.

2. RESULTS

Reciprocal crosses between the dioecious tetraploid *P. fruticosa* obtained from the Teesdale population in the North of England and tetraploid hermaphrodite forms of *P. fruticosa* produced segregating progenies as shown in table 1. The progenies contained hermaphrodites in addition to unisexual types, and in the unisexual members segregation for both sex types occurred only in the progenies where the dioecious parent was female. This thus demonstrates that the female sex is heterogametic.

3. DISCUSSION

Although female heterogamety characterises certain groups in the animal kingdom, such as the Lepidoptera, the birds and some fishes, it is rare in

TABLE 1
*Progeny analyses from crosses between dioecious and hermaphrodite
 tetraploid types of P. fruticosa*

Parentage		Number of progeny	Segregation for sex		
			♀	♂	♀
<i>P. fruticosa</i>	♀ × <i>P. fruticosa</i> micrandra ♀	29	16	11	2
<i>P. fruticosa</i> micrandra	♀ × <i>P. fruticosa</i> ♂	22	0	21	1
<i>P. fruticosa</i>	♀ × <i>P. fruticosa</i> auto 4x* ♀	40	28	5	7
<i>P. fruticosa</i> auto 4x*	♀ × <i>P. fruticosa</i> ♂	81	0	23	58
<i>P. fruticosa</i>	♀ × <i>P. fruticosa</i> auto 4x** ♀	1	0	0	1
<i>P. fruticosa</i> auto 4x**	♀ × <i>P. fruticosa</i> ♂	9	0	9	0
<i>P. fruticosa</i>	♀ × <i>P. fruticosa</i> arbuscula 4x ♂	23	14	8	1

* Autotetraploid induced from open pollinated seed collected from an unknown diploid horticultural variety.

** Autotetraploid induced from seed collected from natural populations in Ontario, Canada.

the plant kingdom. Previously the only examples were known in *Fragaria* (Staudt, *loc. cit.*) but to these can be added the tetraploid shrubby potentilla *P. fruticosa* L. sensu stricto and perhaps the other dioecious members of the taxon, though at present these have not been examined.

Compared with the dioecious tetraploid *Fragaria orientalis* the dioecious tetraploid *Potentilla fruticosa* differs in that the natural populations in Europe are strictly dioecious, whereas the *Fragaria* species is naturally trioecious with hermaphrodites in addition to the unisexual types. From a study of crosses between the three types of *Fragaria orientalis*, Staudt (1967) concluded that sex determination was controlled by three alleles; *su^M* (male suppressing), *su^F* (female suppressing) and *su⁺* (hermaphrodites), and that *su^M* was dominant to *su^F* and *su⁺* and *su^F* was dominant to *su⁺*. These alleles showed tetrasomic inheritance and indicated that the tetraploid species showed characteristics of an autotetraploid with the sex determining alleles in all genomes. With this system, both males and females could be heterozygous for the hermaphrodite allele and could give hermaphrodites in their progenies.

The dioecious tetraploid *Potentilla fruticosa* also shows some autopolyploid features, in lacking differentiating taxonomic characters from diploids, in having 0-3 quadrivalents per cell at meiosis and in having an appreciable amount (40-50 per cent.) of abortive pollen (unpublished data). These features, coupled with the strictly dioecious nature of the N. European populations (Tornblom, 1911; Elkington and Woodell, 1963; Grewal and Ellis, unpublished data), show that only male-determining and female-determining alleles are present and that the alleles must be present in all four genomes as otherwise hermaphrodites would occur. The occurrence of hermaphrodites in the experimental hybridisations suggests that allelism exists in the sex-determining genes and that some are dominant to the hermaphrodite condition and others are recessive. That allelism exists at the morphological level was demonstrated earlier this century by Tornblom (1911), who classified both males and females as weak or strong types, depending on the extent of suppression of the non-functional sex structures.

No attempt has been made to analyse the segregating progenies in relation to this type of allelism as each of the crosses listed involved several individuals of the dioecious *P. fruticosa* probably with different genotypes. However, the variation in the frequencies of hermaphrodites in the progenies obtained could be a consequence of this allelism. Where no hermaphrodites occurred, all sex determinants were possibly of the dominant type; where the hermaphrodites occurred with low frequency, the genotype of the dioecious member possibly contained one recessive determinant; and where the hermaphrodites were more frequent, the dioecious parent possibly contained a preponderance of the recessive determinants.

In another respect the segregation ratios are noteworthy for the consistency with which excess females occurred in those progenies which segregated for males and females. Though the reasons for the inequality in sex ratio have not been established, the observations are fully compatible with previous observations in the natural Teesdale populations where Parbrook (cited by Elkington and Woodell, 1963) recorded 64 per cent. females and 36 per cent. males. These values are similar to the present results where the combined progenies from the female plants (table 2) show that 71 per cent.

TABLE 2
Summary of data from Table 1

Parentage	Number of progeny	Segregation for sex		
		♀	♂	♂
<i>P. fruticosa</i> ♀ × <i>P. fruticosa</i> ♀	93	58	24	11
<i>P. fruticosa</i> ♀ × <i>P. fruticosa</i> ♂	112	0	53	59

of the unisexual plants were females and 29 per cent. were males. Similar inequalities in the proportion of male and female plants were reported in *Fragaria orientalis* by Staudt (1967). In this species the recorded sex ratio was 253 ♀ : 158 ♂ (61.6 per cent. females and 38.4 per cent. males), and Staudt suggested that the excess females could have resulted either from apomixis or preferential development of female determining embryo sacs or female zygotes. These explanations, however, have less validity in *P. fruticosa* as Elkington and Woodell (1963) found that the sex ratio was reversed in populations in Western Ireland, where male plants were twice as frequent as female plants. With these populations it would be desirable to establish whether excess males also occurred in experimental progenies derived from crosses between female plants and hermaphrodites. If so, then perhaps genetical or cytological causal factors could be implicated.

4. SUMMARY

1. Reciprocal crosses between the dioecious N. European form of *Potentilla fruticosa* and a number of tetraploid hermaphrodite forms showed that the female sex was heterogametic.

2. The sex determining genes were thought to be present in all genomes and showed allelism, in that some were dominant and others were recessive to the hermaphrodite condition.

3. In all the progenies the heterogametic parent gave unequal sex ratios in the unisexual plants.

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