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Studies in *Potentilla anserina* L.

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ABSTRACT

The variation of *Potentilla anserina* L. in Britain was studied using material of known wild origin. Both tetraploid and hexaploid cytodemes were found; the latter were much less common but showed no geographical pattern and could not be distinguished with certainty on any morphological character.

INTRODUCTION

Surprisingly little is known about the morphological, cytological and genetical variation of a number of common British plants. In recent years a few such species have been studied by the final-year class at the Botany School, Cambridge University. These studies do not permit an exhaustive investigation of the species concerned, but they often bring to light a number of interesting facts which could form the basis of a more complete study. The work reported here on *Potentilla anserina* L. was carried out during the summers of 1967 and 1968 by the final-year class and the authors. We are grateful to a number of colleagues who helped to collect samples for cultivation.

The experimental taxonomic study of *Potentilla anserina* by Rousi (1965) provided a very useful basis for our work, and should be consulted for further information on the taxonomy, morphology and distribution of the species. Most of the 51 samples which Rousi studied came from Europe and North America. Three of these proved to be hexaploid ($2n=42$) and the rest tetraploid ($2n=28$). The hexaploids had a low pollen fertility (about 20%) and failed to set seed, while the tetraploids had a much higher pollen fertility (60–98%) and produced fertile seed. The only British plant studied by Rousi (from Nether Poppleton, near York) was hexaploid and had irregular meiosis and low pollen fertility (19·9%).

Very few of the herbarium specimens of British *P. anserina* in the Cambridge Herbarium (**CGE**) have fruit, and the scarcity of fruit in natural populations has been observed by several botanists. This suggested to us that in Britain the hexaploid might be commoner than the tetraploid, although the reverse is true for the two areas (Finland and California) studied in detail by Rousi (1965).

MATERIALS

The living plants used in this study are listed in Table 1. Most have been cultivated in the Cambridge University Botanic Garden; the remainder include two large population samples from Fulbourn Fen and Wicken Fen, Cambridgeshire.

TABLE 1. LIST OF PLANTS USED, WITH DETERMINED PLOIDY LEVEL AND FRUIT PRODUCTION

Plant Ref. No.	Botanic Garden Ref. No.	Locality of Origin	10 km National Grid Ref.	Ploidy Level	No. of plants Counted	Fruit Production
1	137B/67	Pegwell Bay, Kent	61/36	4*x*	2	+
2	156A/67	Rubha Bàn, Tighnabruaich, Argyll	16/97	4*x*	2	+
3	156B/67	Ardlamont Point, Argyll	16/96	4*x*	1	+
4	161B/67	Ovingdean, near Brighton, Sussex	51/30	4*x*	1	+
5	156D/67	Hayley Lane, Cambs.	52/25	4*x*	1	+
6	180C/67	Roadside S. of Berwick, Northumberland	46/05	4*x*	1	+
7	180D/67	Saltmarsh below Arnside Knott, Westmorland	34/47	4*x*	1	–
8	180E/67	Royston Heath, Herts.	52/33	4*x*	1	+
9	198A & B/67	Farland Point, Great Cumbrae, Bute	26/15	6*x*	3	+
10	198C-E/67	St. Catherine's, Loch Fyne, Argyll	27/10	4*x*	3	+
11	205/67	Icklingham, Suffolk	52/77	4*x*	1	+
12	156C/67	Ditton Park Wood, Cambs.	52/65	4*x*	1	+
13	184/66	Akureyri, N. Iceland	—	4*x*	1	–
14	137D/67	Porth Ysgo, Llanfaelrhys, Lleyn Peninsula, Caernarvonshire	23/22	6*x*	1	+
15	262A/67	Ynys Las, Cardiganshire	22/69	4*x*	1	+
16	226A/67	Upper Teesdale, Co. Durham	35/92	4*x*	1	+
17	226B/67	Selside, Ingleborough, W. Yorks.	34/77	4*x*	1	+
18	226C/67	Austwick, W. Yorks.	34/76	4*x*	1	+
19	274B/67	Nether Poppleton, near York	44/55	6*x*	2	0
20	246/67	Lake Bohinj, Julian Alps, Jugoslavia	—	4*x*	1	+
21	276/67	Everingham, E. Yorks.	44/84	4*x*	1	+
22	339G/67	Troutdale, near Scarborough, N.E. Yorks.	44/98	4*x*	2	+
23	339F/67	St. Keverne, Lizard, Cornwall	10/72	4*x*	1	+
24	339D/67	Rubha Carriag, Nandarrach, Colonsay	—	4*x*	1	–
25	339E/67	Port Askaig, Islay	16/46	4*x*	1	+
26	339C/67	Rubh An Dobhrain, Colonsay	16/49	4*x*	1	+
27	339B/67	Machair, Vragang, Colonsay	16/39	4*x*	1	–
28	339A/67	Scalasaig, Colonsay	—	4*x*	1	+
29	262E/67	Eriswell, W. Suffolk	52/77	4*x*	2	–
30	—	Burwell, Cambs.	52/56	6*x*	3	–
FF	—	Fulbourn Fen, Cambs.	52/55	4*x*	1	+
WF	—	Wicken Fen, Cambs.	52/57	4*x*	1	+
ER	—	Eriswell, W. Suffolk	52/77	4*x*	5	–

In last column: + = fruit produced 0 = no fruit produced – = not flowering

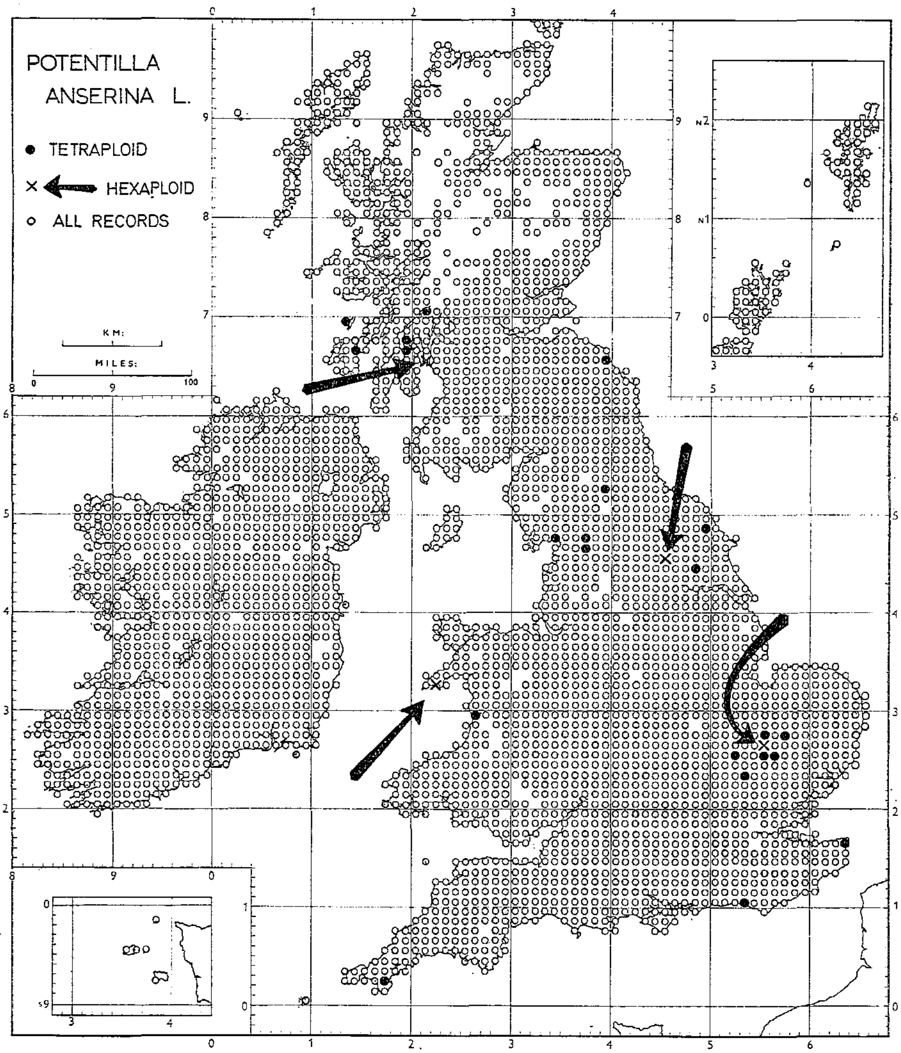

FIGURE 1. Distribution of *Potentilla anserina* L. in the British Isles. By permission of the Botanical Society of the British Isles, and Thomas Nelson & Sons Ltd., taken from their *Atlas of the British Flora*, and updated by the Biological Records Centre, Monks Wood Experimental Station, Abbots Ripton, Huntingdon.

TAXONOMY AND MORPHOLOGY

Rousi (1965) considers a number of morphological characters, both vegetative and reproductive, selecting particularly those characters which previous authors have used to distinguish taxa within the *P. anserina* aggregate. Three such characters were studied in the British material and a brief summary of the results follows.

1. LENGTH/BREADTH RATIO OF TERMINAL LEAFLET

Rousi found that this ratio 'was lower in all three hexaploid plants than in the related tetraploids from the same or neighbouring areas'. The figures for the two populations sampled by us were:

	No. of plants	Range	Mean	Standard Deviation	Standard Error of Mean
Fulbourn	73	1·4–3·5	2·02	0·41	0·048
Wicken	57	1·3–3·9	2·21	0·49	0·065

In each case a single leaf was measured. The range of values for plants in cultivation (1·5–3·1, Table 2) is somewhat less than that found in a single population sample. The hexaploids have values of 2·0 or below, which supports Rousi's finding, but, as many of the tetraploids also have values below 2·0, this character alone cannot be used to distinguish the two ploidy levels.

2. NUMBER OF TEETH

The number of teeth on one side of the terminal leaflet, plus the terminal tooth, was counted. The figures for the population samples were:—

	No. of plants	Range	Mean	Standard Deviation	Standard Error of Mean
Fulbourn	36	9–16	12.97	1·30	0·22
Wicken	36	8–18	11·64	1·85	0·31

In each case a single leaf was used. Again the ranges of values for the population samples are greater than the range of single values for the plants in cultivation (Table 2), and there is no correlation between number of teeth and ploidy level. However, the two lowest values (7 and 8) are on plants from native localities in the western Scottish islands (plants nos. 25 and 24 respectively).

3. EPICALYX SEGMENTS

The following grading was adopted in order to measure the variation in the toothing of the epicalyx segments:

Grade 0—all segments entire
Grade 1—some but not all segments toothed
Grade 2—all segments toothed or laciniate, but not exceeding the calyx
Grade 3—all segments laciniate, some or all exceeding the calyx

The results for the population samples were as follows:—

	Total no. of flowers	Grade				Mean Grade
		0	1	2	3	
Fulbourn	10	0	1	9	0	1·90
Wicken	50	1	5	39	5	1·96

The plants in cultivation showed the same sort of range for this character as the population samples, but the west Scottish and Lizard plants (25, 26, 28, 23) showed low grades of 0 or 1, in contrast to the hexaploid from Yorkshire (19a) and the tetraploid from Teesdale (16), both of which showed grade 3 (Table 2).

TABLE 2. MORPHOLOGICAL CHARACTERS

In several cases, the sample cultivated consists of more than one original plant. Such cases are indicated in the remaining tables by adding a, b, etc. to the reference number.

Plant Ref. No.	Terminal Leaflet: Length/breadth ratio	Terminal Leaflet: No. of teeth	Epicalyx Grade
1	2·1	—	—
2	2·2	—	—
6	2·1	—	—
7	1·5	—	—
9a (6x)	1·7	—	—
9b (6x)	1·6	—	—
14 (6x)	2·0	—	1
15	2·1	13	2
16	2·0	12	3
17	2·8	10	2
18	1·7	12	2
19a (6x)	1·6	12	3
19b (6x)	1·9	10	3
20	1·9	11	2
21a	2·0	12	—
21b	1·6	12	2
22a	2·4	11	0
22b	2·4	11	2
22c	3·1	—	2
22d	2·2	11	0
23	2·1	12	1
24	2·0	8	—
25	1·8	7	0
26	1·5	10	1
27	1·7	—	—
28	2·7	—	1

Further evidence of a difference in the epicalyx between coastal Scottish and lowland English populations can be seen by comparing the following figures scored in the field in August 1968 with those given above for the Wicken and Fulbourn populations:

	Total no. of flowers	Grade 0	Grade 1	Grade 2	Grade 3	Mean Grade
Loch Linnhe, Fort William	10	1	6	2	1	1·3
Lochaline, Morvern, Argyll	10	0	8	2	0	1·2
North outskirts of Oban (1)	10	4	6	0	0	0·6
North outskirts of Oban (2)	10	0	6	4	0	1·4

A noteworthy feature of the coastal Scottish populations is that they approach the arctic *P. anserina* subsp. *egedii* (Wormsk.) Hiit., which is characterised by entire or shallowly toothed epicalyx segments and a low number of teeth on the terminal leaflet. Plant no. 13 from northern Iceland is referable to this subspecies, and plants from Shetland in the Cambridge Herbarium (**CGE**) are identifiable as subsp. *egedii* using the diagnostic description provided by Rousi. Rousi has found populations in Finland with a mixture of *anserina* and *egedii* characters, a condition which is approached by some of the coastal Scottish populations. The occurrence of such intermediate populations, and the ease of production of artificial hybrids between subspp. '*anserina*' and '*egedii*' which Rousi found, support his conclusion that the appropriate rank for these two taxa is that of subspecies. If the variation between these two subspecies is more or less continuous, and has a geographical basis, then the two subspecies may be regarded as the relatively extreme end-points of a topocline.

CHROMOSOME NUMBERS

P. anserina is not easy cytological material, and precise counts are difficult to make. Approximate counts are usually sufficient for a determination of the ploidy level, however, and as most of our counts are approximate the ploidy level rather than the chromosome number is given in Table 1. All our counts were made from squash preparations of root tips. Root tips of *P. anserina* can easily be obtained by allowing runners to root in water. The root tips were pre-treated with α-bromonaphthalene for 2 hours, fixed in Carnoy's solution and stained in alcoholic hydrochloric acid carmine (Snow 1963).

Four of the 33 samples which have been counted are hexaploids, the rest being tetraploid (Table 1, Fig. 1). One of the hexaploid samples (19) is from the same place as Rousi's British hexaploid. The other three hexaploids are from Great Cumbrae, Bute (9), Lleyn Peninsula, N. Wales (14) and Burwell, Cambridgeshire (30). There is thus no clear pattern in the distribution of the two ploidy levels in Britain. This agrees with Rousi's finding that his 3 hexaploids were not confined to any one area.

In the relatively few instances where more than one plant per sample was counted, there was no evidence for mixed populations of tetraploids and hexaploids.

POLLEN FERTILITY

Pollen fertility was estimated by counting 100–200 pollen grains stained with cotton blue in lactophenol. In contrast to Rousi's results we have found that the pollen fertility of a single plant varies at different times of the year (Table 3), and that the fertility of plants in a population differs at any one time (Table 4). Because of variation in pollen fertility during the flowering season, it is important to note the date when the pollen fertility is determined. The 3 counts made for plant 25 (Table 3) suggest that the pollen fertility falls off towards the end of the flowering season. Nevertheless, counts made late in the season may still show a high fertility (e.g. 97% for plant no. 24 on 23/7/68).

The range of pollen fertility in single populations is unusually large (Table 4) and may result from individual plants losing their pollen fertility at different rates. The difference in average pollen fertility between the Fulbourn Fen and

TABLE 3. POLLEN FERTILITY (% OF 'GOOD' GRAINS)

Plant Ref. No.	Date	Fertility	Date	Fertility	Date	Fertility
1a	July 67	45	27/5/68	92		
1b	July 67	86	27/5/68	99		
2a	July 67	80	27/5/68	97		
2b	July 67	86				
2c	July 67	35				
3	July 67	64	27/5/68	97		
4	July 67	90	27/5/68	92		
5	July 67		27/5/68	48		
6a	July 67	76	27/5/68	75		
6b	July 67	62				
7	July 67	62				
8	July 67	30	27/5/68	35		
9a	July 67	28	27/5/68	14		
9c	July 67	11				
10a	July 67	45	27/5/68	58		
10b	July 67	47	27/5/68	50		
10c	July 67	47	27/5/68	35		
11	July 67	58	July 67	87	27/5/68	93
12	July 67	86				
13	July 67	32	27/5/68	79		
14	6/7/68	11				
15	6/7/68	98				
16	6/7/68	95				
17	28/6/68	39				
18	27/5/68	26				
19a	26/7/68	2				
19b	15/8/68	10				
20	28/6/68	80				
21a	27/5/68	86				
21b	28/6/68	98				
22a	6/7/68	98				
22b	28/6/68	97				
22c	6/7/68	85				
22d	28/6/68	98				
22e	9/7/68	97				
23	6/7/68	97				
24	23/7/68	97				
25	6/7/68	97	19/7/68	83	26/7/68	68
26	6/7/68	97				
28	9/7/68	97	19/7/68	90		

TABLE 4. VARIATION IN POLLEN FERTILITY IN POPULATIONS SAMPLED

Population	Date	No. plants sampled	Range of fertility	Average fertility
Ditton Park Wood, Cambs.	31/7/67	12	37–94%	79%
Fulbourn Fen, Cambs.	25/7/68	35	20–97%	53%
Wicken Fen, Cambs.	25/7/68	30	41–99%	82%

Wicken Fen populations is also striking, and indicates that there is variation between populations in this character, as well as within populations.

This variation in pollen fertility in *P. anserina* tends to obscure the clear-cut difference between the pollen fertility of tetraploids and hexaploids found by Rousi (1965). The pollen fertility of our hexaploids is 2–28%, while the lowest value recorded for the tetraploids is 26% (plant no. 18). Plants with pollen fertilities of 25–35% could be tetraploid or hexaploid and this is not a safe way of determining the ploidy level unless several pollen fertility counts are made at different times of the year. The majority of the tetraploids have a maximum pollen fertility above 80%, but some plants (e.g. 8 and 10) have a consistently low pollen fertility, indicating a marked degree of male sterility. Rousi (1965) records similar male sterility in one of the populations which he studied.

FRUIT PRODUCTION

Almost all the tetraploid plants in cultivation which have flowered have also produced fruit (Table 1). Of the hexaploids, both plants from Nether Poppleton (19a and b) have not produced fruit, but all three plants from Great Cumbrae (9a–c) and the single plant from the Lleyn Peninsula (14) have fruited. Fruit production by these hexaploids is unexpected and needs to be further investigated. Rousi mentioned the possibility that this might occur, although he did not publish any evidence for it.

Rousi selfed a number of plants and found that they were all self-incompatible. We have found the same results with the 11 plants (10 tetraploids, 1 hexaploid) which we have tested. Each of these plants has fruited in open cultivation, and a cross between plants 15 and 16, made at the same time as the self-pollinations, has produced 10 achenes. It is reasonable to conclude that the failure of fruit production following self-pollination results from self-incompatibility rather than sterility.

MODES OF REPRODUCTION

P. anserina is capable of vigorous vegetative spread, and the difficulty of finding fruiting material in the field raises the question of the relative importance of sexual and asexual modes of reproduction under natural conditions. In both the Wicken and Fulbourn Fen populations fruiting heads were found after a careful search, but could easily have been overlooked. At Wicken, *P. anserina* was found growing on a track, in tall grass near the track, and at the margin of the track, but it was only at the margin that any quantity of fruit was found. Most of the plants grown in pots in Cambridge fruited well during the summer of 1968, but those grown in beds fruited poorly in 1968, although they were vegetatively very vigorous that year and had fruited the previous year. The plants in pots also flowered much more freely than those in the beds. These facts suggest the possibility that sexual reproduction is much reduced in plants which are growing very vigorously (and reproducing asexually) because of poor flower production. *P. anserina* does not appear to have a very definite flowering period in Cambridge, and flowers may be produced sporadically from May to September. Flowering in the wild is also often rather poor, less than about 10% of the plants being in flower at any one time, and those that are flowering having only one or two flowers open at once.

In addition to poor flowering, low fertility of the flowers which are produced might also reduce fruit production. It is of interest that fruits were easier to find in the Wicken population than in the Fulbourn population, and that the latter had a much lower average pollen fertility. However, plants with consistently low pollen fertilities (such as the three plants from St Catherine's, Loch Fyne, Argyll (10a–c)) have produced good fruit, and there is no evidence that female sterility is associated with male sterility.

The achenes produced by the plants in cultivation are fertile, and up to 80% germination has been obtained using the method suggested by Rousi (1965). Evidence for the successful sexual reproduction of *P. anserina* in the field is scanty, but seedlings were found in a damp meadow at Soham, Cambridgeshire in July 1968. The seedlings occurred in a small compact group, suggesting that they had grown from the achenes of a single fruiting head.

The precise rate of vegetative spread of *P. anserina* is not known, but runners up to 1m in length may be produced during one growing season. Vegetative reproduction is undoubtedly very important in producing the dense, and sometimes quite extensive, patches of *P. anserina* which are commonly seen in the field. Although long-distance dispersal of vegetative parts may occur, it is likely that sexual reproduction is more important than asexual for the establishment of new populations.

DISCUSSION

The three morphological characters investigated all vary somewhat on different parts of the same plant and may vary widely within a single population. This severely limits their use as simple taxonomic characters and suggests that statistical methods should be applied if these characters are to be studied in more detail. It is clearly important to have sizeable population samples with which to compare the data collected from individual plants from different localities. There are no clear discontinuities in the morphological variation of *P. anserina* in Britain, and the high variability of single populations tends to obscure the geographical pattern of the variation.

The low and variable pollen fertility of *P. anserina* is unusual for a species which reproduces sexually and is not agamospermous. Some other species of *Potentilla* (e.g. *P. tabernaemontani*) are pseudogamous (Smith 1963), but there is no evidence of this in *P. anserina.* The low pollen fertility could be interpreted as indicating an increasing emphasis on vegetative reproduction as opposed to sexual reproduction. It is possible that mutations leading to reduced male fertility also give increased vegetative vigour and hence are not selected against as strongly as they would be in species which relied on sexual reproduction alone.

The distribution of the hexaploids in Britain does not show any obvious pattern (*cf* Fig. 1), and this agrees with Rousi's suggestion that hexaploids have had a polytopic origin from the tetraploids. Their reproduction is almost entirely by vegetative propagation and their high sterility probably prevents them from spreading far from their source of origin.

CONCLUSION

Both hexaploid and tetraploid plants of *P. anserina* occur in Britain, the latter being much the commoner. The two cytodemes cannot be distinguished with absolute certainty by any character other than the chromosome number. However, plants exhibiting all or most of the following characteristics are likely to be hexaploid: low pollen fertility, poor achene production, relatively broad terminal leaflets, high tooth number, and laciniate epicalyx segments. Rousi's single sample of *P. anserina* from Britain was atypical in being hexaploid and could give a misleading impression of the species in this country. This illustrates the danger of making generalisations based on insufficient evidence. Much remains to be discovered about the variation of *P. anserina* in Britain, and more information about its ecology and mode of reproduction in the field is highly desirable. In particular, coastal populations in natural habitats in the north and west could be much more effectively sampled to see to what extent a topocline between subsp. *anserina* and subsp. *egedii* exists in Britain.

REFERENCES

ROUSI, A. (1965). Biosystematic studies on the species aggregate *Potentilla anserina* L. *Ann. Bot. Fenn.*, **2**: 47–112.

SMITH, G. L. (1963). Studies in *Potentilla* L. I. Embryological investigations into the mechanism of agamospermy in British *P. tabernaemontani* Aschers. *New Phytol.*, **62**: 264–282.

SNOW, R. (1963). Alcoholic hydrochloric acid carmine as a stain for chromosomes in squash preparations. *Stain Technol.*, **38**: 9–13.