Cytotaxonomy of *Jasione montana* L. in the British Isles

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ABSTRACT

The chromosome number of populations of *J. montana sensu lato* from the British Isles is reported. β chromosomes are shown to occur at low frequency in certain populations. The significance of the position and frequency of occurrence of chiasmata in these populations is discussed.

INTRODUCTION

Cytological studies of the genus *Jasione*, Campanulaceae, are fragmentary. The only systematic survey which has been undertaken is that of Kovanda (1968), who surveyed forty-six Continental populations of *Jasione montana* L. *J. montana* is the most widespread species in the genus and the only representative naturally occurring in Britain. No chromosome studies have been published relating to British material.

Most European counts for *J. montana sensu lato* are either n=6 or 2n=12 (Table 1). However, a sand dune ecotype from Schleswig-Holstein, *Jasione montana* L. var. *litoralis* Fr. was reported as having n=7 by Wulff (1937). Continental workers have been unable to refind this population or any other example of the variety (see Kovanda 1968). This variety occurs in Britain and its variation pattern and taxonomic status have been investigated by Parnell (1980). This paper presents a report of a cytological investigation of eleven populations of *J. montana sensu lato* in the British Isles.

TABLE 1. RECORDED CHROMOSOME NUMBERS FROM *JASIONE MONTANA* L. *SENSU LATO*

Species	n	2n	Author
Jasione montana		12	Contandriopoulos (1966)
Jasione montana	6		Delay (1969)
Jasione montana		12	Gadella (1966)
Jasione montana	6	12	Gadella & Kliphuis (1966)
Jasione montana		12	Gadella & Kliphuis (1968)
Jasione montana		12	Gadella & Kliphuis (1970)
Jasione montana		12	Kliphuis & Wieffering (1972)
Jasione montana		12	Kovanda (1968)
Jasione montana		12	Majovsky (1970)
Jasione montana	6		Poddubnaya-Arnoldi (1934)
Jasione montana		12	Podlech & Damboldt (1963)
Jasione montana	6		Rosen (1932)
Jasione montana	6		Sugiura (1940)
Jasione montana	6		Sugiura (1942)
Jasione montana	6		Wulff (1937)
Jasione montana L. var. *bracteosa* Willk. Syn. *Jasione blepharodon* Boiss. & Reuter		12	Bjorqvist *et al.*(1969)
Jasione montana var. *litoralis* Fr.	7		Wulff (1937)
Jasione montana L. var. *montana*. Syn. *Jasione montana* L. var. *maritima* Dufour		12	Contandriopoulos (1966)
Jasione montana L. var. *montana*. Syn. *Jasione montana* L. var. *maritima* Dufour	6		Delay (1967)

MATERIALS AND METHODS

The populations examined came from a wide geographical range within the British Isles (Table 2). At each locality young, entire, bractless inflorescences were taken from ten plants selected at random. The inflorescences were fixed, immediately on collection, in freshly prepared Carnoy's fluid (six parts ethanol: one part acetic acid: three parts chloroform) and stored at −20°C until required. Anther squashes were made in either aceto-carmine (A.C.) or lactopropionic orcein (L.P.O.) following the standard procedure of Dyer (1963), c.f. Darlington & La Cour (1962).

From each successful squash, chromosome number, chiasma frequency, positions of chiasmata and the occurrence of any abnormalities were noted. Chiasma frequency and position differ at different stages of the meiotic cycle and therefore these data were recorded only at diakinesis. It was originally hoped to obtain twenty chiasma frequency counts from at least ten plants from each population, but difficulties were encountered due to the very low frequency of detection of cells in diakinesis. The mean chiasma number per cell and the percentage of terminalized chiasmata are calculated for each plant from a site.

Voucher specimens of the sampled populations are deposited in Aberdeen University Herbarium (**ABD**).

RESULTS AND DISCUSSION

GENERAL

Very few meiotic abnormalities were noted. Occasional, isolated, pollen mother cells showed either multivalent or univalent formation. Neither multivalent nor univalent formation was a constant feature of any anther or plant.

An unusual but ubiquitous feature of meiosis in *J. montana* was the lagging of the smallest homologous pair of chromosomes at first metaphase (Plate 3, 1 & 2). This chromosome pair often began to separate only after the rest of the chromosome complement had entered early first anaphase. This feature of the meiotic process of *J. montana* was also noted by Delay (1969) in Continental material.

CHROMOSOME NUMBER AND β CHROMOSOMES

The results of the survey (Table 2) show that all plants counted had n=6 (Plate 3). No evidence for the n=7 cytotype of Wulff (1937) was found. These results reinforce the general picture of uniformity in chromosome number found in Continental material of *J. montana* by Kovanda (1968) and other authors (Table 1). However, this survey also revealed that two populations (SO5 and C23) of *J. montana* var. *litoralis* possessed β chromosomes (Plate 3, 2 & 4). This may explain Wulff's (1937) count of n=7 in *J. montana* var. *litoralis*. The other population of this taxon sampled (C25) did not have β chromosomes nor were any found in any other population of *J. montana sensu lato* sampled.

The β chromosomes detected were all telocentric and much smaller than any of the normal chromosome complement. They did not separate out with the normal chromosome complement at first metaphase nor did they undergo homologous pairing at the same time as the normal chromosome complement. The staining intensity of both β chromosomes and the normal chromosome complement was the same and both seemed equally heterochromatic. Cells with one or two β chromosomes were detected and their behaviour was not uniform at meiosis. In cells with one β chromosome, β chromosome division occurs at first anaphase in the pollen mother cells. In plants with two β chromosomes the β choromosomes were found either to lie alongside each other at pachytene (possibly pairing), or, more commonly, to remain unpaired. In the two populations containing the plants with the β chromosones the mean frequency of occurrence of β chromosomes was 33%. There was no noticeable effect of β chromosomes on plant morphology or upon the meiotic behaviour of the normal chromosome complement.

CHIASMA FREQUENCY AND POSITION

The results of the analysis of chiasma frequency and position are shown in Table 3. The populations are listed in order of increasing chiasma frequency. Considerable variation was detected both in

TABLE 2. LOCATION, CHROMOSOME NUMBER AND OCCURRENCE OF CHROMOSOMES IN ELEVEN POPULATIONS OF *JASIONE MONTANA* L. *SENSU LATO*

Site No.	Grid Reference	General location	Number of plants scored	Chromosome number (*n*)	Number of plants with β chromosomes	Number of β chromosomes
S05	16/813.376	Kintyre,v.c. 101	6	6	2	1β, 2β.
S06	16/599.065	Kintyre,v.c. 101	7	6	0	0
S07	16/628.062	Kintyre,v.c. 101	7	6	0	0
S08	16/658.074	Kintyre,v.c. 101	10	6	0	0
S09	16/694.077	Kintyre,v.c. 101	10	6	0	0
S14	25/182.561	Wigtown,v.c. 74	5	6	0	0
S22	16/883.289	Arran,v.c. 101	6	6	0	0
C15	10/603.419	Cornwall,v.c. 1	3	6	0	0
C23	30/033.845	Dorset,v.c. 9	6	6	2	2β, 2β.
C25	30/039.856	Dorset,v.c. 9	10	6	0	0
I01	T/11.03	Wexford,v.c. H12	10	6	0	0

TABLE 3. MEAN CHIASMA NUMBER PER CELL; PERCENTAGE OF TERMINALIZED CHIASMATA, AND RECOMBINATION INDEX VALUES IN ELEVEN POPULATIONS OF *JASIONE MONTANA* L. *SENSU LATO*

Site No.	Total pollen mother cells scored	Total plants scored	Mean chiasma frequency per cell	Standard error	Mean percentage terminalized chiasmata per cell	Standard error	Recombination index
S14	5	2	6·4	1·1	67·2	0·6	12·4
S08	13	4	7·1	0·4	66·6	7·6	13·1
C25	9	3	7·2	0·9	53·4	2·5	13·2
S06	9	3	8·1	1·4	51·0	6·2	14·1
S07	11	4	8·2	0·5	32·8	8·6	14·2
C15	4	1	8·3	—	42·0	—	14·3
C23	10	6	8·3	0·2	51·0	5·5	14·3
I01	9	5	8·3	0·4	51·0	5·5	14·3
S09	8	3	8·5	0·4	57·9	5·8	14·5
S22	7	2	8·7	0·3	57·9	5·8	14·7
S05	15	4	9·7	0·3	73·8	1·8	15·7
All			8·4	0·2	56·3	1·7	14·1

mean chiasma frequency (6·5–9·5 chiasmata per cell, i.e. 1·07–1·62 chiasmata per bivalent) and in the mean percentage of terminalized chiasmata (33%–74% per cell). Analysis of the raw data showed that total chiasma number is not significantly correlated with the percentage of terminalized chiasmata ($r=0·15$ $p>0·05$) and that the two, therefore, vary independently.

Various authors have indicated the role of recombination as a source of genetic variation. Grant (1965) states that "Recombination generates most of the differences between individuals in a population. . .". Chiasma frequency has a central role in determining recombinant frequency. Stebbins (1971) and Davis & Heywood (1963) indicate that a raised chiasma frequency results in an increase in genetic variability and a low chiasma frequency has the opposite effect. Additionally, Stebbins (1971) states that localization of chiasmata will "protect" certain areas of the chromosome by reducing the amount of crossing over. Such effective localization of chiasmata may occur if chiasmata are terminally placed on the homologues.

This study has shown that in pollen mother cells of *J. montana* (Plate 3, 4) the mean number of chiasmata per cell is approximately eight (*i.e.* only 1·4 chiasmata per bivalent) and that on average 56% of these chiasmata occur in terminal positions (Table 3). The combination of these factors will tend to reduce the amount of genetic recombination which can occur.

A measure of the amount of genetic recombination possible in a sexually reproducing population is given by the Recombination Index (R.I.). The index was defined by Darlington (1963) as the sum of the haploid chromosome number and the average number of chiasmata per meiotic cell. In normally outbreeding species Stebbins (1971) and Gibbs *et al.* (1975) view a low R.I. as an alternative to predominant self fertilization as a means of assuring a temporary reduction in the amount of genetic recombination. As can be seen (Table 3) the R.I. of *J. montana* was found to vary between 12·4 and 15·7. No R.I. values are available for other *Jasione* species but intergeneric comparisons indicate that these R.I. values are low. For example, Gibbs *et al.* (1975) found that *Senecio* species had R.I. values in the range 22·6–44·8, Stebbins *et al.* (1946) found R.I. values of 42·2, 44·0 and 53·0 for *Agropyron, Elymus* and *Sitanion* respectively and Garber (1956) found that *Collinsia* had R.I. values in the range 14·7–16·6.

Stebbins *et al.* (1946), Garber (1956) and Gibbs *et al.*(1975) have shown that the linkage between the R.I. and degree of outcrossing is well established. *J. montana* is an outbreeding species but a generally low R.I. and high percentage of terminalized chiasmata may enable successful recombinants to be conserved.

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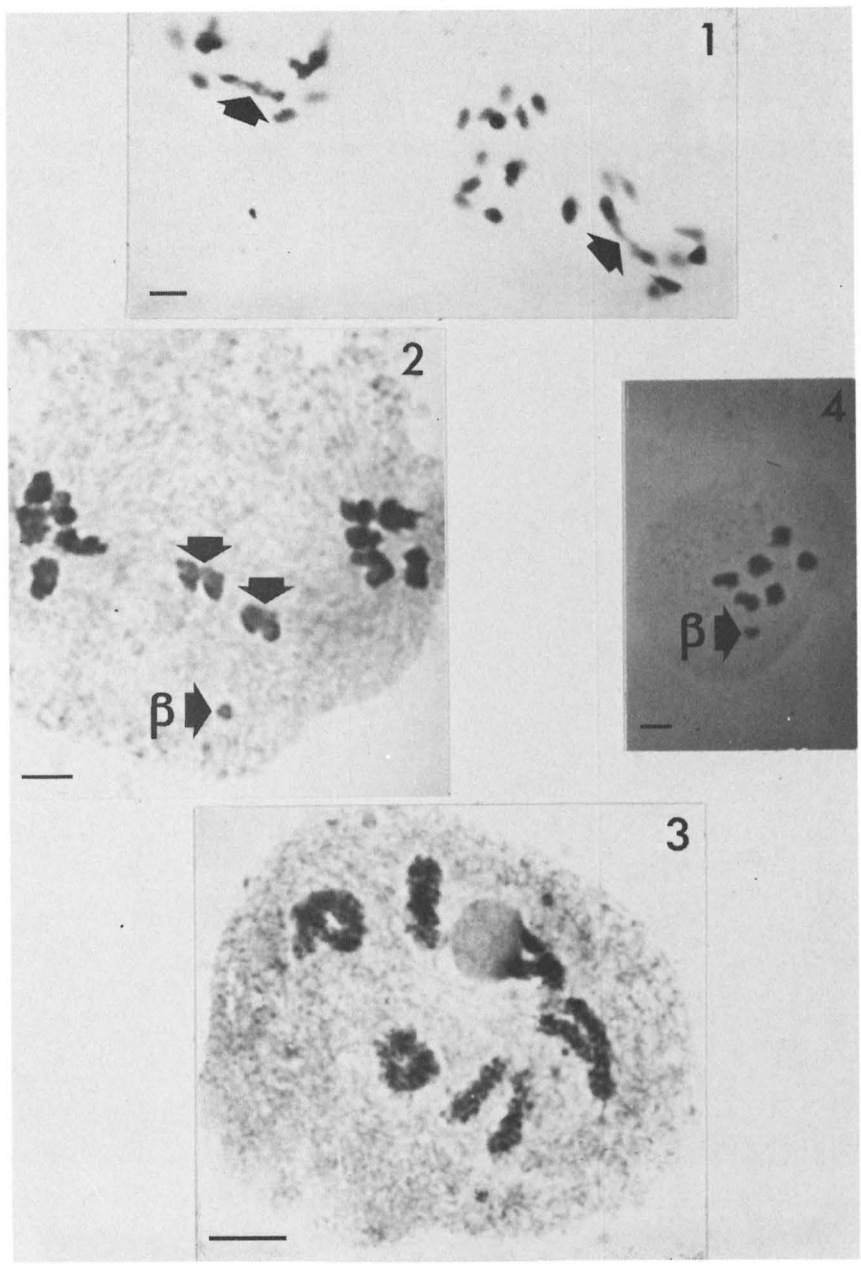

PLATE 3. Photographs of chromosomes of *Jasione montana* L. (1) *J. montana* var. *montana*, $n=6$. All chromosomes are at first anaphase but a laggard bivalent (arrowed) has only just begun division. (2) *J. montana* var. *litoralis*, $n=6+1\beta$. All chromosomes are in first anaphase but laggard chromosomes (arrowed) have not yet moved to the poles of the cell. One β chromosome is present (β). (3) *J. montana* var. *montana*, $n=6$. All bivalents at diakinesis. (4) *J. montana* var. *litoralis*, $n=6+1\beta$. All chromosomes are in first telophase. One β chromosome is present. Scale bars on photographs equal 5μm.