The frequency and meiotic behaviour of structural chromosome variants in natural populations of *Allium schoenoprasum* L. (wild chives) in Europe

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Meiotic analysis of 1017 plants of *Allium schoenoprasum*, sampled as adults from 18 natural populations in Britain and continental Europe, revealed that 35 (3.4 per cent) were heterozygous for one or more major structural chromosome mutations. Nineteen different interchanges, 11 different inversions, one deletion, and one supernumerary chromosome segment were found. There was no significant difference between British and continental European populations in the frequency of chromosomal variants.

There was considerable variation in meiotic behaviour between different interchanges. On average, quadrivalent formation occurred in 68 per cent meiocytes, but the range (from 13 to 95 per cent) was wide. In five interchange heterozygotes, chiasma formation in the interstitial segments occurred in a high proportion of multivalents. In three interchange heterozygotes, a significant excess of chain quadrivalents were in alternate orientation. In the inversion heterozygotes, the frequency of reverse loop chiasma formation was relatively low, occurring, on average, in 6 per cent meiocytes (with a range from 3 to 13 per cent). The pollen and ovule fertilities of inversion heterozygotes were little affected, but those of many interchange heterozygotes were significantly depressed.

The distribution of structural chromosome mutations throughout the genome was not random. A disproportionately high frequency involved the acrocentric, nucleolar–organizer chromosome pair.

Keywords: *Allium schoenoprasam*, chromosome variants, non-random chromosome rearrangements, meiotic analysis, population cytogenetics.

Introduction

Structural chromosome rearrangements have considerable potential for modifying patterns of genetic recombination at meiosis, thereby conserving or creating specific gene combinations. When structural chromosome mutants occur at a low frequency in natural populations (e.g. White, 1961; Jacobs, 1977) they are probably transient and have little or no evolutionary importance. There are, however, a number of well-documented examples of species in which structurally variant chromosomes occur at a high frequency in natural populations. A few of these chromosomal polymorphisms are known to be maintained by natural

selection, e.g. the paracentric inversion sequences in *Drosophila* (reviewed by Williamson, 1972; Wallace, 1981), but other factors such as meiotic drive (e.g. Wilby & Parker, 1988; Parker *et al.*, 1988), a high level of asexual reproduction (e.g. Brandham & Johnson, 1977), or a rapid mutation rate (e.g. Wilby & Parker, 1987) may contribute towards the spread of chromosomal variants. In some species, structural heterozygotes appear to have an advantage in ecologically marginal populations, which are often subject to inbreeding (Lewis & John, 1957; James, 1965; Wedberg *et al.*, 1968; Bloom, 1977; see also Charlesworth *et al.*, 1977).

Allium schoenoprasum L. (Liliaceae) is a bulbous, perennial plant which reproduces both vegetatively by the production of daughter bulbs on short rhizomes and sexually by the production of seed. In Britain, the species is uncommon and most of its disjunct popula-

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tions are comparatively small and occur in open, rocky habitats often on thin soils. Flowering and seed production are infrequent in some of these populations (Bougourd, 1977; Stevens, 1985). By contrast, in the Alps and Pyrenees in continental Europe, *A. schoenoprasum* is more abundant, and typically occurs in densely vegetated valley mires and water meadows. Flowering is prolific in these localities. It appears, therefore, that British populations of *A. schoenoprasum* are somewhat more ecologically marginal than their continental counterparts. Preliminary cytogenetic studies of British populations indicated that moderate levels of chromosome heterozygosity were present in at least two sites (Bougourd, 1977). In this paper we compare the incidence and meiotic behaviour of chromosome variants in populations of this species from Britain and continental Europe.

Materials and methods

Sampling and cultivation

In September 1981 and August 1982, mature bulbs of *A. schoenoprasum* were sampled at spaced intervals of at least 1 m from eight natural populations in Britain and 10 in continental Europe (Fig. 1). The plants were cultivated in Levington Universal compost in 8 cm diameter pots and maintained under controlled glasshouse conditions with supplementary lighting and heating to give a 16-h day and to maintain a minimum temperature of 16°C. The plants were transferred outside for 2–3 months during the winter to receive a cold chill which stimulates the production of flower buds.

Cytological methods

Meiosis was studied in pollen mother cells (PMCs), which were obtained from fresh or fixed (in 1:3 acetic–alcohol) flower buds and stained in 2 per cent lactopropionic orcein. Mitosis was studied in root tip cells, which were pretreated in 0.05 per cent colchicine for 2.5 h, fixed in 1:3 acetic–alcohol, and stained by the Feulgen method.

Ten PMCs at first metaphase (M1) were examined per plant for multivalents, indicative of interchange heterozygosity, and asymmetrical bivalents, suggestive of deletion, supernumerary segment or pericentric inversion. One hundred PMCs at first anaphase (A1) were examined per plant for dicentric bridges with acentric fragments of constant size, suggestive of paracentric inversion heterozygosity. [Chiasmata are not localized in *Allium schoenoprasum*, so the fragments associated with dicentric bridges formed by U-type

exchange are expected to be of unequal length (Jones, 1968).]

Karyotype analysis was carried out on suspected chromosomal heterozygotes, together with a more detailed analysis of their meiotic behaviour. The frequency of multivalent formation was scored for each interchange heterozygote, in a random sample of between 6 and 159 M1 PMCs, and the shape (ring or chain), orientation (alternate or adjacent), and presence or absence of interstitial chiasmata were noted for each multivalent. (The centromeres of the seven pairs of metacentric chromosomes in *A. schoenoprasum* are indistinguishable at M1, so the orientation of quadrivalents with interstitial chiasmata could not be determined.) To avoid bias, the meiotic behaviour of each interchange heterozygote was recorded only from slides where the interchange chromosomes could be identified in all M1 PMCs observed. For each paracentric inversion heterozygote the frequency of loops and dicentric bridges at A1 and the sizes of the associated acentric fragments, were scored in a random sample of 100–450 PMCs.

Fertility testing

The male and female fertilities of 16 different structural chromosome heterozygotes from six populations were estimated by scoring the percentage stainability of 250–300 pollen grains per plant in Alexander's Differential Stain (Alexander, 1969), and by counting seed set per capsule following manual cross-pollination of 12–20 flowers per plant with fertile pollen from a basic homozygote. The fertilities of each structural chromosome mutant were compared with the mean fertilities of 10–20 control plants (basic homozygotes) from the same population using a modified *t*-test (Sokal & Rohlf, 1981) following arcsin square root transformation of percentage pollen stainability data, and square root transformation of seed set data. The fertility tests of chromosome mutants and control plants were carried out simultaneously in a uniform environment.

Results

The basic karyotype

Allium schoenoprasum is normally diploid with eight pairs of chromosomes that range in size from 5.6 to 8.3 μm at colchicine-metaphase (Fig. 2a). Chromosome pairs 1–7 are metacentric, while pair 8 is acrocentric and carries the nucleolar–organizer region (NOR). During normal male meiosis, the eight bivalents usually have a total of between 15 and 17 non-localized chiasmata (Fig. 2b).
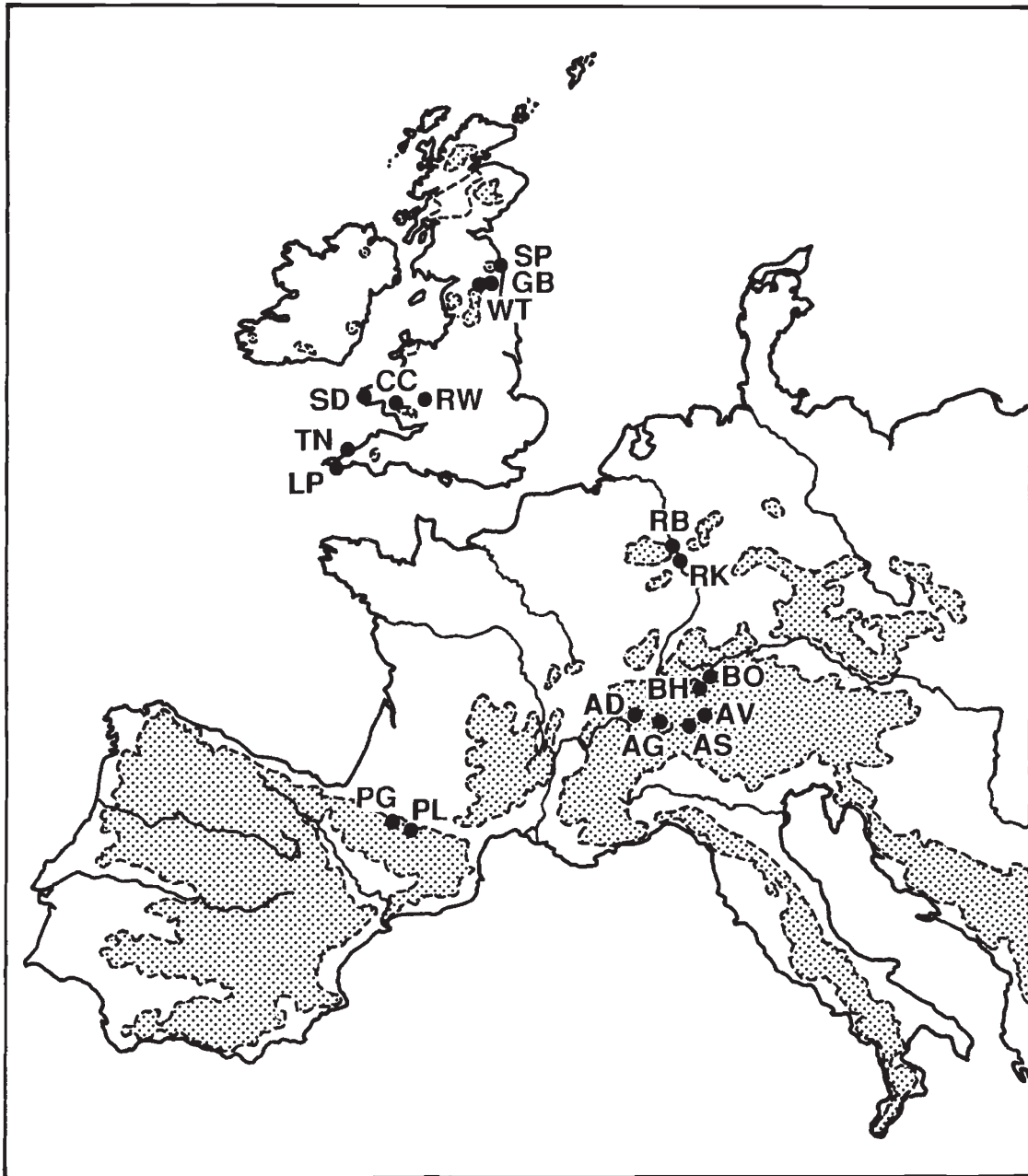
Fig. 1 Distribution of the 18 sampling sites of *Allium schoenoprasum*. Shaded areas = land over 500 m.
Britain: SP = Spindlestone; GB = Great Bavington; WT = Walltown; RW = River Wye; CC = Carreg Cennen; SD = St David's
Head; TN = Tintagel; LP = Lizard Peninsula.
Rhine: RB = Brohl; RK = Krummenwerth.
Bodensee: BO = Oberxell; BH = Hegne.
Alps: AD = Davos; AG = Gamchi; AS = Sertig Dorfli; AV = Vrin.
Pyrenees: PG = Gabas; PL = Lac de Tracens.

Numerical variants

All but one of 1017 plants analysed meiotically were
diploid. A single, highly sterile, triploid plant was found
in the population sample of 144 plants from the Lizard
Peninsula, England.

B-chromosomes were found in 22 per cent of plants
from the River Wye, Wales, and in both populations
from the French Pyrenees at frequencies of 11 per cent
at the Gabas site and 74 per cent at the Lac de Tracens
site (Stevens, 1985). The morphology and behaviour of
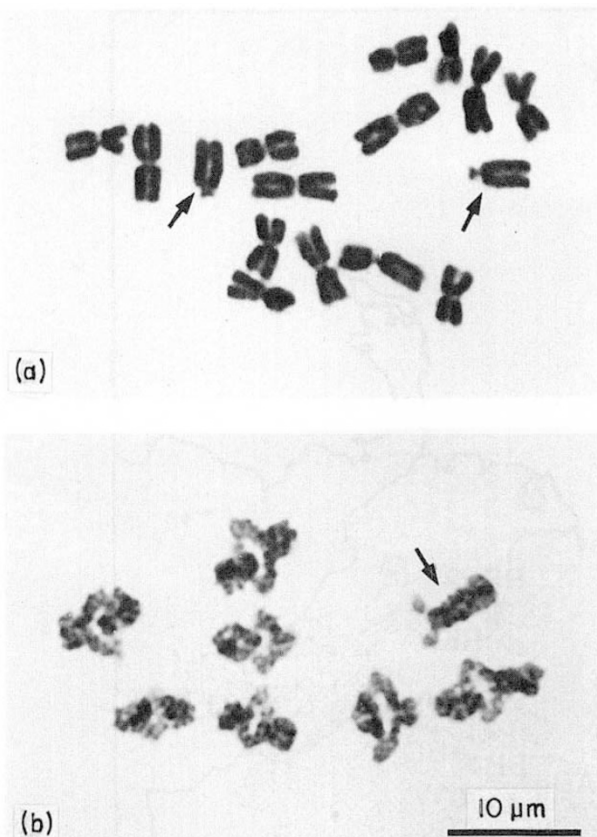the B-chromosomes are discussed elsewhere (Bou-

Fig. 2 Standard chromosome complement of *Allium schoenoprasum*: (a) colchicine-metaphase, (b) metaphase 1 of male meiosis (arrows indicate acrocentric chromosome pair).

gourd & Parker, 1975, 1979a,b; Stevens, 1985; Holmes & Bougourd, 1989).

Structural mutants

A total of 35 structural chromosome heterozygotes was found, two of which were heterozygous for two different chromosomal rearrangements (Table 1). No novel structural chromosome homozygotes were found, although homozygotes for symmetrical re-arrangements would rarely have been detectable. The frequency of plants carrying one or more chromosomal rearrangements was slightly higher in the British than in the continental European population samples (3.8 and 2.8 per cent respectively), but this difference is not statistically significant ($\chi^2_{(1)} = 0.43$, $P > 0.5$).

The 37 rearrangements identified comprise 23 interchanges, 12 paracentric inversions, one deletion and one supernumerary chromosome segment (Table 1).

Interchanges. Meiotic and karyotypic analyses revealed that the 23 interchanges consisted of 19 different rearrangements. Four bulbs sampled from the

Walltown population, Northumberland, England, all carried the same rearrangement, as did two bulbs sampled from the population near Tintagel, Cornwall, England (Fig. 3a and b). It is likely that the local spreading of these two interchange types has occurred asexually rather than sexually because no interchange homozygotes were found and heterozygotes for both rearrangements had very low fertilities (see Table 3, interchanges 2–5 and 18–19).

Eight of the 19 different interchanges detected involved an acrocentric (pair 8) chromosome (e.g. Fig. 3c); the remaining 11 involved two metacentrics from pairs 1–7. Therefore, eight of the 38 chromosome breaks (21.1 per cent) occurred in an acrocentric. If the distribution of chromosome breaks is random, and the expected frequency per chromosome is calculated on the basis of relative chromosome length at colchicine-metaphase, 10.7 per cent of the breaks would be expected to occur in an acrocentric. The observed frequency (21.1 per cent) is significantly greater than this ($\chi^2_{(1)} = 4.26$, $P < 0.05$), which suggests that chromosome breaks that result in viable gametes are distributed non-randomly in *A. schoenoprasum*.

Detailed analysis of M1 was possible for 15 different interchange types (suitable slides, with no unclassifiable PMCs, were unavailable for the remaining four). The results are summarized in Table 2 and examples shown in Fig. 4. On average, quadrivalent formation occurred in 68 per cent PMCs, but the range (from 13 to 95 per cent) was wide. Eight of the 15 different interchanges analysed involved an acrocentric chromosome, and interstitial chiasmata were especially common in four of these, occurring in over 60 per cent of multivalents (interchanges 1, 2–5, 7, 21). A similar level of chiasma formation in the interstitial segments occurred in only one of the seven interchange types that involved two metacentrics (interchange 18–19). The presence of an interstitial chiasma reduces the maximum number of genetically balanced meiotic products from four to two.

When chiasmata were restricted to the pairing segments, none of the eight interchanges that involved an acrocentric chromosome formed ring quadrivalents, whereas six of the seven that involved two metacentrics formed both ring and chain multiples. This reflects the virtual absence of crossing over in the short arms of the acrocentric chromosomes in *A. schoenoprasum*.

Alternate and adjacent orientations of ring quadrivalents were observed in approximately equal frequencies in all six heterozygotes that formed at least occasional ring multiples (Table 2). This is expected if the four centromeres of a quadrivalent orientate in pairs at random (John & Lewis, 1965). By contrast, there was significant heterogeneity between interchange types in the orientation behaviour of chain

Table 1 Frequency and classification of meiotically detectable structural chromosome heterozygotes in natural populations of *Allium schoenoprasum* from Britain and continental Europe

Population	Total plants	Number (%) of heterozygotes	Types of mutation			
			Int.	Inv.	Del.	SS
Britain						
Great Bavington	11	0 (0.0)	—	—	—	—
Spindlestone	25	1 (4.0)	1	—	—	—
Walltown	61	5 (8.2)	4	—	1	—
River Wye	175	4 (2.3)	1	2	—	1
Carreg Cennen	63	0 (0.0)	—	—	—	—
St David's Head	72	4* (5.6)	3	3	—	—
Lizard Peninsula	144	6 (4.2)	6	—	—	—
Tintagel	78	4 (5.2)	4	—	—	—
Subtotal	629	24 (3.8)	19	5	1	1
Continental Europe						
Gabas	27	1 (3.7)	—	1	—	—
Lac de Tracens	20	0 (0.0)	—	—	—	—
Davos	23	0 (0.0)	—	—	—	—
Sertig Dorfli	24	0 (0.0)	—	—	—	—
Gamchi	34	0 (0.0)	—	—	—	—
Vrin	37	2 (5.4)	1	1	—	—
Oberxell	44	1 (2.3)	1	—	—	—
Hegne	59	1 (1.7)	1	—	—	—
Krummenwerth	53	4 (7.5)	—	4	—	—
Brohl	67	2 (3.0)	1	1	—	—
Subtotal	388	11 (2.8)	4	7	0	0
Grand total	1017	35 (3.4)	23	12	1	1

*Two plants from St David's Head each carried two different chromosomal mutations.

Int. = interchange, Inv. = inversion, Del. = deletion, SS = supernumerary chromosome segment.
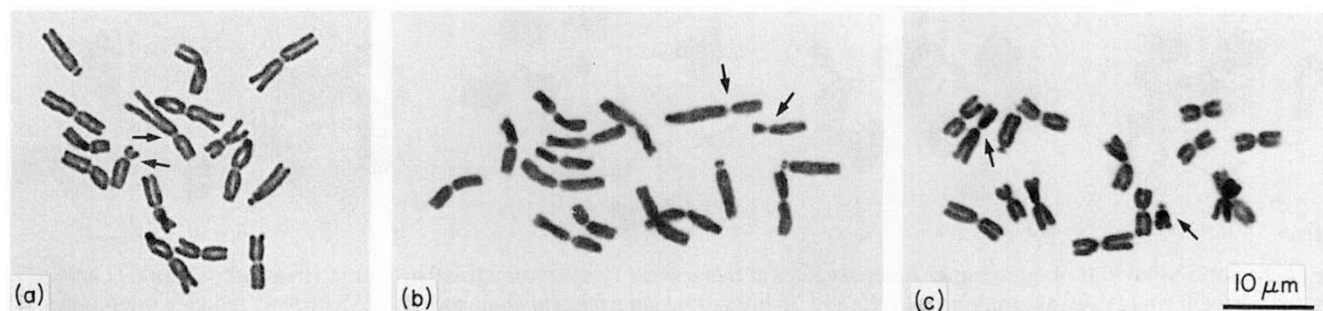
Fig. 3 Chromosome complements of interchange heterozygotes: (a) interchange 18, (b) interchange 19, (c) interchange 14 (arrows indicate interchange chromosomes).

quadrivalents (heterogeneity $\chi^2_{(4)} = 20.13$, $P < 0.001$, omitting data from interchanges with sample sizes of less than 10 chains). Chain quadrivalents tended to orientate alternately in interchanges 10, 14 and 20, whereas in interchange 18–19, adjacent orientation was more frequent (Table 2).

All the interchange heterozygotes detected were healthy, morphologically normal plants. However, the majority of those for which controlled fertility estimates were obtained had significantly reduced fecundities, with levels of pollen stainability ranging from 62 to 90 per cent of normal, and levels of seed set as low as

Table 2 Meiotic behaviour of interchange heterozygotes scored at metaphase 1 (M1)

Interchange number	Population	Chromosome pairs involved	Total M1 scored	Number (%) M1 with IV	8 II	III+I	Ring IV alt.	Ring IV adj.	Chain IV alt.	Chain IV adj.	III+I	Ring IV	Chain IV
1	Spindlestone	ac. mc.	12	3 (25)	8	—	—	—	—	—	1	—	3
2–5	Walltown	ac. mc.	159	20 (13)	137	—	—	—	—	—	2	—	20
6	River Wye	mc. mc.	23	17 (74)	6	—	6	8	2	—	—	1	—
7	St David's Head	ac. mc.	13	11 (85)	2	—	—	—	2	1	—	8	—
10	Lizard Peninsula	mc. mc.	21	20 (95)	1	—	5	4	9	2	—	—	—
12	Lizard Peninsula	ac. mc.	62	19 (31)	43	—	—	—	8	11	—	—	—
13	Lizard Peninsula	mc. mc.	55	49 (89)	6	—	20	21	4	4	—	—	—
14	Lizard Peninsula	ac. mc.	27	21 (78)	6	—	—	—	15	6	—	—	—
15	Lizard Peninsula	mc. mc.	30	21 (70)	9	—	8	8	3	1	—	—	1
17	Tintagel	mc. mc.	35	34 (94)	2	—	10	13	4	5	—	1	—
18–19	Tintagel	mc. mc.	78	73 (94)	5	—	—	—	9	17	—	—	47
20	Vrin	ac. mc.	57	51 (89)	6	—	—	—	40	11	—	—	—
21	Oberxell	ac. mc.	6	5 (83)	1	—	—	—	1	1	—	—	3
22	Hegne	mc. mc.	11	6 (55)	5	—	2	2	1	1	—	—	—
23	Brohl	ac. mc.	7	3 (43)	1	3	—	—	3	—	—	—	—

Xmata = chiasmata, I = univalent, II = bivalent, III = trivalent, IV = quadrivalent, alt. = alternative orientation, adj. = adjacent orientation, ac. = acrocentric, mc. = metacentric.
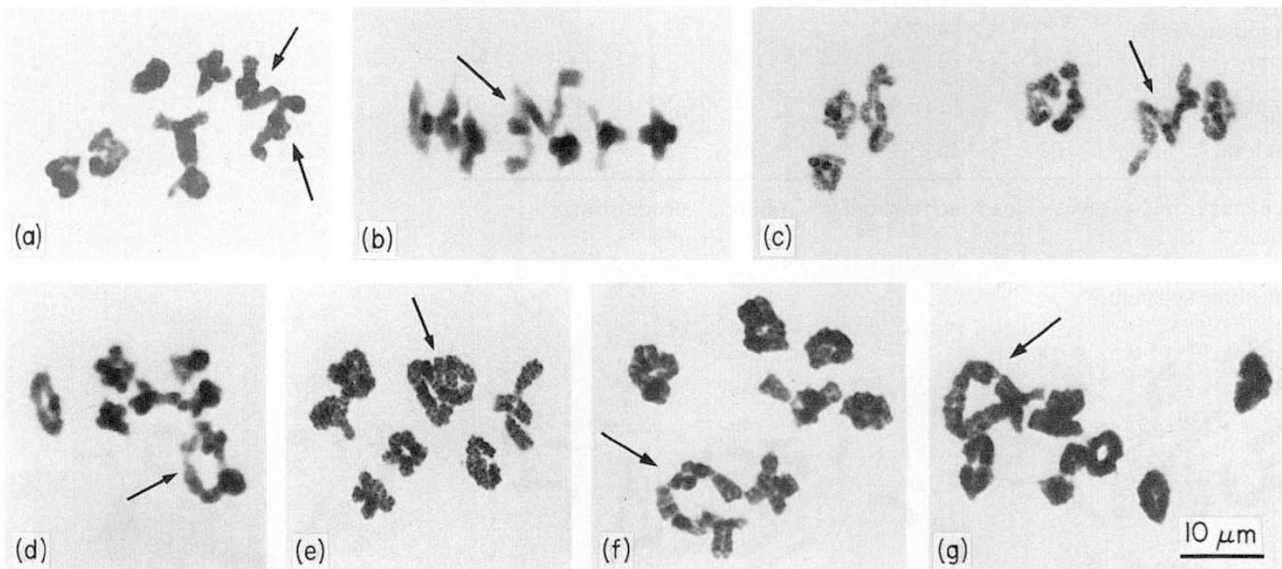
Fig. 4 Meiotic behaviour of interchange heterozygotes at metaphase 1: (a) asymmetrical bivalents, (b) and (c) alternate chain IVs, (d) adjacent ring IV, (e) alternate ring IV, (f) and (g) interstitial chiasmata in chain and ring IVs (arrows indicate interchange chromosome associations).

39 per cent of normal (Table 3). It should be noted that the female, and to a lesser extent male, fecundities of normal chromosomal homozygotes from the three populations in Northumberland, England (Great Bavington, Spindlestone and Walltown) are extremely low (for unknown reasons). Thus the fertility levels of some chromosomal heterozygotes from these sites, although low, are not significantly lower than those of the population controls.

Inversions

When crossing-over occurs in a reverse pairing loop in a paracentric inversion heterozygote, the length of the

Table 3 Pollen and ovule fertilities of chromosome heterozygotes. For each heterozygote, stainability of 250–300 pollen grains, and seed set in 12–20 capsules, were scored. Each observation was compared with the mean of 10–20 control plants from the same population using a modified t-test (Sokal & Rohlf, 1981). Population codes are given in Fig. 1

Mutant	Population	Pollen fertility				Ovule fertility			
		Percentage of pollen stainability	As percentage of controls	t	d.f.	Seed set per capsule	As percentage of controls	t	d.f.
Interchange									
1	SP	68.5	73.1	− 3.572**	18	0.4	117.6	0.337	9
2–5	WT	41.8	72.8	− 0.866	19	0.0	—	− 0.714	9
8	SD	74.0	80.9	− 3.590**	13	2.5	65.4	− 2.758*	13
9	SD	65.9	72.1	− 4.748***	13	2.3	60.2	− 3.229**	13
11	LP	78.8	90.3	− 2.134*	19	3.1	87.6	− 0.264	18
12	LP	61.3	70.3	− 4.339***	19	2.5	70.6	− 1.006	18
13	LP	76.2	87.4	− 2.490*	19	1.4	39.4	− 2.530*	18
16	TT	62.0	71.4	− 3.760**	14	—	—		
17	TT	76.3	87.9	− 2.120	14	2.9	83.8	− 0.883	14
18–19	TT	53.6	61.8	− 4.662**	14	1.6	46.2	− 2.591*	14
Inversion									
1	RW	0.0	—	− 15.533***	15	4.9	122.8	1.616	15
2	RW	89.2	93.4	− 0.854	15	4.1	102.8	0.206	15
3/4	SD	79.4	86.6	− 2.753*	13	4.2	109.9	0.662	13
Deletion	WT	53.5	93.2	− 0.270	19	0.0	—	− 0.714	9
Supernumeray segment	RW	93.0	97.4	− 0.058	15	4.4	110.3	0.745	15

$* = P < 0.05; ** = P < 0.01; *** = P < 0.001.$

acentric fragment associated with the resulting A1 dicentric bridge (or loop) is always constant, and equal to the length of the inverted segment plus twice the length of the distal segment. Slight variation of fragment lengths is, however, inevitable following squash preparations of meiosis due to differential stretching or folding of the fragments.

Data on the meiotic behaviour at A1 of plants carrying the 12 paracentric inversions are given in Table 4 and examples are shown in Fig. 5. The small number of fragments of a non-uniform length (e.g. 5.5 μm, inversion 1) are probably caused by U-type exchange. Abnormalities indicative of U-type exchange were observed in 33 per cent of 1017 plants studied, in an average of 1.67 per cent PMCs per affected plant (Stevens, 1985).

It is likely that inversions 9 and 10 from Krummenwerth, West Germany, are the same because both involve an acrocentric chromosome, and they have similar meiotic characteristics (Table 4).

In total, four (27 per cent) of the 11 different inversion types found involved an acrocentric chromosome. This is considerably more than the expected frequency of 10.7 per cent, although the expected number (1) is too small for a statistical test of significance to be performed.

The products of reverse loop chiasmata occurred in a low proportion of PMCs in the 11 inversion types detected (mean = 6 per cent PMCs, range = 3–13 per cent PMCs). The fertilities of three inversion heterozygotes, including the plant carrying inversions 3 and 4, were tested, and the results are given in Table 3. Seed set was not reduced. However, the plant carrying inversions 3 and 4 had a significantly reduced pollen stainability, and the plant carrying inversion 1 was completely male sterile, but this was probably for reasons unconnected with the chromosomal rearrangement.

Deficiency

A single, phenotypically normal plant from the Walltown population, Northumberland, England, carried a deletion of the entire short arm of an acrocentric chromosome (Fig. 6). This arm constitutes 1.02 per cent of the haploid genome at colchicine-metaphase, it is at least partly heterochromatic, and it carries the NOR. A maximum of one rather than two nucleoli

Table 4 Meiotic behaviour of paracentric inversion heterozygotes scored at anaphase 1 (A1). Population codes are given in Fig. 1

Inversion number	Population	Chromosome involved	Number A1 scored	Number A1 with			Fragment length (μm)												Number (%) A1 with RLC
				B+F	L+F	BB+FF	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	7.0	
1	RW	ac.	390	12	2	0	—	—	—	—	8	3	2	—	—	1*	—	—	13 (3)
2	RW	mc.	411	16	0	0	—	—	1*	—	—	—	—	—	1	7	7	—	15 (4)
3†	SD	mc.	410	49	1	2	—	—	—	—	—	22	29	1	—	—	—	—	52 (13)
4†	SD	mc.	410	19	0	0	—	7	3	—	8	1	—	—	—	—	—	—	19 (5)
5	SD	mc.	147	14	0	0	—	1*	—	9	4	—	—	—	—	—	—	—	13 (9)
6	AG	ac.	241	10	0	0	—	—	9	1	—	—	—	—	—	—	—	—	10 (4)
7	AV	ac.	110	4	0	0	—	—	—	5	—	—	—	—	—	—	—	—	5 (5)
8	RB	mc.	238	10	0	1	—	—	—	—	1	4	—	—	—	—	—	5	10 (4)
9	RK	ac.	450	23	0	0	—	7	16	—	—	—	—	—	—	—	—	—	23 (5)
10	RK	ac.	363	27	0	0	3	12	6	—	6*	—	—	—	—	—	—	—	21 (6)
11	RK	mc.	100	11	0	0	—	11	—	—	—	—	—	—	—	—	—	—	11 (11)
12	RK	mc.	200	14	0	0	1*	—	2	2	9	—	—	—	—	—	—	—	13 (7)

*Bridge and fragment formations probably caused by U-type exchange. †Inversions 3 and 4 both occurred in the same plant.
B+F = dicentric bridge and acentric fragment; L+F = loop and acentric fragment; BB+FF = double dicentric bridge and two acentric fragments of equal length; RLC = reverse loop chiasma; ac. = acrocentric; mc. = metacentric.

occurred in root tip cells. The pollen and ovule fertilities of the deletion heterozygote were not significantly below those of the control plants from Walltown (Table 3). Relatively large (> 1.0 per cent of the genome) viable deficiencies are known to occur in a number of other diploid plant and animal species (Finch, 1983) but this is believed to be the first report of such a mutation in A. schoenoprasum.

Supernumerary chromosome segment

A single plant from the River Wye population, Wales, was heterozygous for a mitotically stable supernumerary chromosome segment situated terminally on the short arm of an acrocentric chromosome distal to the NOR which was visible as a secondary constriction (Fig. 7a and b). The segment was approximately 1.24 μm long at colchicine-metaphase, causing a threefold increase in the length of the standard acrocentric short arm. Its presence did not appear to affect fertility (Table 3).

A probable chiasmate association was observed between the supernumerary chromosome segment and a metacentric bivalent in one M1 PMC (out of 80 examined) (Fig. 7c). This suggests that the segment may have arisen from a viable duplication–deficiency gamete produced by an interchange heterozygote carrying an unequal translocation involving the short arm of an acrocentric chromosome.

Discussion

In natural populations of A. schoenoprasum from Britain and continental Europe, 3.6 per cent of mature plants have been shown to be heterozygous for meiotically detectable structural chromosome rearrangements. This finding reinforces the conclusion reached by Parker et al. (1988) from cytological studies on Scilla autumnalis (Ainsworth et al., 1983; see also Guillén & Ruiz Rejón, 1984) and Rumex acetosa (Wilby & Parker, 1989) that the frequency of structural rearrangement in plants may be at least an order of magnitude higher than that of between 1 in 200 and 1 in 500 generally thought to be present in natural populations (White, 1973, 1978). High levels of karyotypic heterogeneity have also been reported in members of the Aloineae (Brandham, 1974, 1976). However, both in A. schoenoprasum and in the other species mentioned here, the variability is superimposed on a karyotype that appears to be fundamentally stable over a wide geographic range.

In A. schoenoprasum, there does not appear to have been selection for particular structural chromosome rearrangements in the populations studied. Moreover,
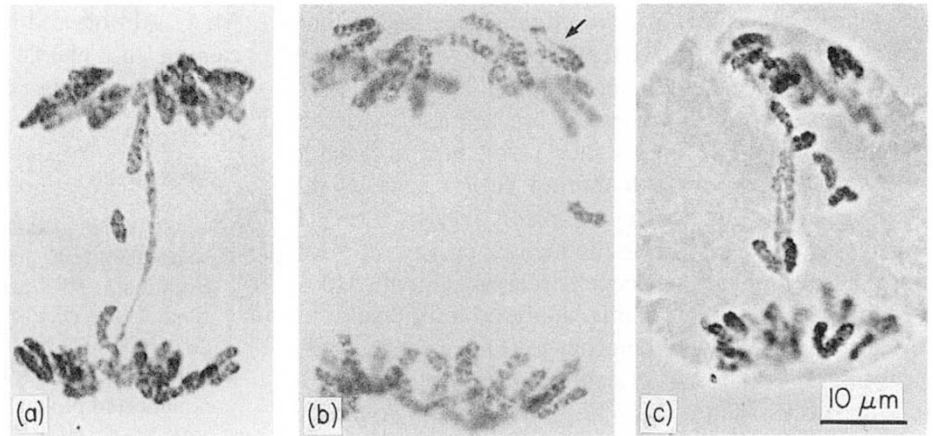
Fig. 5 Meiotic behaviour of paracentric inversion heterozygotes at anaphase 1: (a) bridge and fragment, (b) loop (arrowed) and fragment, (c) double bridge and two fragments.
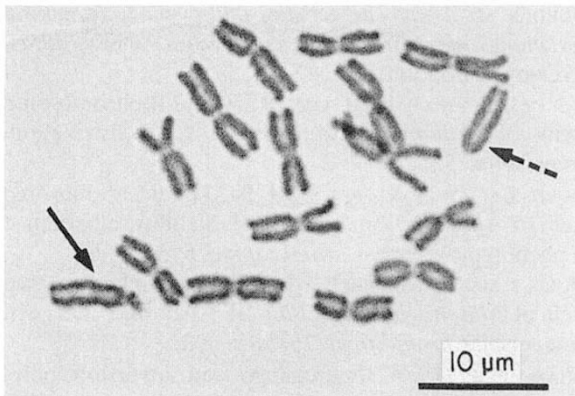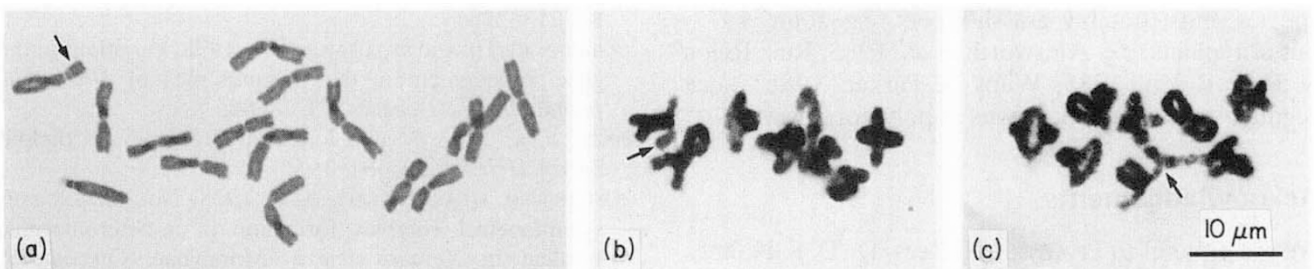

Fig. 6 Chromosome complement of deletion heterozygote (hatched arrow indicates deleted acrocentric and solid arrow indicates normal acrocentric).

lead to enhanced selection pressure for chromosomal mechanisms that help conserve co-adapted gene complexes (e.g. Rees, 1961b). However, our recent work on inbreeding depression in *A. schoenoprasum* suggests that the British populations are no more inbred than the continental ones (Stevens & Bougourd, 1988). In addition, the relatively high frequency of non-localized chiasmata that are characteristic of meiosis in this species may render it somewhat unsuitable for the establishment of interchange and inversion polymorphism.

Significantly more structural chromosome variants involved the acrocentric nucleolar–organizer chromosome pair than would have been expected on the basis of relative chromosome lengths at colchicine-metaphase. Data from the preliminary cytological investigation of *A. schoenoprasum* suggest a similar non-random distribution of breakpoints (Bougourd, 1977). Apparently non-random distributions of inversions (e.g. Dobzhansky & Sturtevant, 1938) and interchanges (e.g. Savage & Bigger, 1976) have been observed in other organisms. It is possible that the acrocentric chromosomes of *A. schoenoprasum* are particularly prone to breakage, or alternatively that a higher proportion of structural mutations involving the acrocentrics is viable.

there was no significant difference between the British and the continental European populations in the frequency of major structural rearrangements. The British populations are small and more ecologically marginal, and one might have expected them to be relatively inbred. Enforced inbreeding of a normally outbreeding species could result in an increased rate of spontaneous breakage (e.g. Rees, 1961a) or it could

Fig. 7 Chromosome complement and meiotic behaviour at M1 of supernumerary chromosome segment heterozygote: (a) colchicine-metaphase, (b) 8 bivalents, (c) 6 bivalents plus probable IV (arrows indicate supernumerary chromosome segment).

Meiotic analysis is a more effective technique than mitotic analysis for the detection of paracentric inversion and interchange heterozygotes. However, pericentric inversion heterozygotes are difficult to detect by either technique unless they result in a noticeable shift in the position of a marker region such as the centromere or nucleolar–organizer region. The 12 inversions detected during the meiotic survey reported here did not include pericentric rearrangements. However, three of 1239 plants analysed mitotically by Bougourd (1977) were heterozygous for a centric shift, presumably caused by pericentric inversion.

The successful detection of paracentric inversions at first anaphase depends upon the formation of reverse pairing loops in which crossing-over occurs during pachytene. Although reverse loops have been observed in a few species (e.g. Watanabe & Noda, 1974) and the products of reverse loop chiasmata have been observed in many more (e.g. Brandham, 1977), reverse loop pairing is not universal. Instead straight, non-homologous pairing may occur across mutually inverted segments (Fletcher & Hewitt, 1978), or the segments may remain unsynapsed. Paracentric inversions that never, or only rarely, form reverse loop chiasmata will not have been detected during the present study.

A supernumerary chromosome segment has previously been reported in *A. schoenoprasum* (Bougourd, 1977). However, this segment was mitotically unstable. It occurred in about 60 per cent of root tip cells of a single individual amongst the progeny of a cross between one plant from the River Wye, Wales, and one from the Lizard Peninsula, England; neither parent carried the extra segment. This segment, like the segment described here, was also attached to the short arm of an acrocentric chromosome; it resembled an enlarged satellite region and varied in length from 1.3 to 5.4 µm at colchicine-metaphase. Unstable segments, resembling enlarged satellites, have been reported in other species (Marchant & Brighton, 1971; Brandham, 1975). The supernumerary segment reported here is believed to be the first report of a stable supernumerary segment in *A. schoenoprasum*. In some species, most notably grasshoppers (e.g. John, 1973) but also plants (e.g. Ainsworth *et al.*, 1983; Ruiz Rejón & Ruiz Rejón, 1985; Wilby & Parker, 1988), such segments occur in populations as polymorphisms.

Acknowledgements

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