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Inheritance and fitness effects of a pericentric inversion and a supernumerary chromosome segment in *Muscari comosum* (Liliaceae)

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The inheritance and the effects on fitness of a pericentric inversion and a supernumerary chromosome segment (SCS) involving the second chromosome pair of *Muscari comosum*, have been analysed in an experimental population. Whereas the inversion is inherited in a Mendelian fashion through the female side, the SCS shows a powerful accumulation mechanism ($k = 0.796$). Cases of nonrandom pollination were observed in homozygous bulbs for the standard chromosomes (+ +) and also in those homozygous for the inverted chromosomes (ii), which may be caused by a certain rate of self-pollination. The different karyotypes for both the inversion and the SCS showed similar values for several life-history traits related to female fitness, such as bulb weight, number of fruits, number of seeds and seed weight. However, plants carrying the inversion had heavier bulbs than those lacking it. The significance of these observations is discussed in relation to the maintenance of the two types of polymorphism in natural populations.

Keywords: accumulation mechanism, fitness effects, inheritance pattern, *Muscari comosum*, pericentric inversion, supernumerary segment.

Introduction

Although pericentric inversion polymorphism has frequently been reported in natural populations of animals, particularly in rodent and grasshopper species (White, 1973), it has rarely been found in plants, with the exception of a few cases in maize (Morgan, 1950) and some Liliaceae such as *Allium thunbergii* (Watanabe & Noda, 1974) or *Muscari comosum* (Bentzer & Ellmer, 1975). One of the most widespread cases of polymorphism for pericentric inversion reported in plants was found in *M. comosum* L. (Liliaceae) ($2n = 18$), where all natural populations analysed from the Mediterranean region (from Greece to the Canary Islands) showed this polymorphism in the second longest chromosome pair (Bentzer & Ellmer, 1975; Ruiz Rejón & Oliver, 1981; Ruiz Rejón *et al*., 1990). In addition, this same chromosome pair shows a polymorphism for an euchromatic supernumerary chromosome segment (SCS) (Ruiz Rejón *et al*., 1987), a kind of polymorphism especially frequent in natural populations of grasshoppers (Hewitt, 1979; Camacho *et al*., 1984) and plants (Rhoades, 1942; Ruiz Rejón & Ruiz Rejón, 1985; Jamilena *et al*., 1991, 1995).

The pericentric inversion reaches quite high frequencies in natural populations of *Muscari comosum* ($q_i = 0.34$ on average), and there are only slight between-population frequency differences over the geographical distribution of the polymorphism, although the inverted chromosomes tend to be less frequent in populations located at ecological borders (Ruiz Rejón *et al*., 1990). The SCS is also present over the whole geographical range, but at a much lower frequency, and thus some populations lack it (Ruiz Rejón *et al*., 1990).

It is of interest to identify the factors that determine the maintenance of these polymorphisms in natural populations. The analysis of the association of these polymorphisms with certain enzymatic loci,

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and the calculation of the F_{I}, F_{IS}, F_{ST} and F_{IT} *F*-statistics (Wright, 1951), provided indirect evidence that both types of polymorphism could be maintained by means of natural selection (Ruiz Rejón *et al*., 1990). Although *M. comosum* is a bulbous member of the family Liliaceae, its reproduction is entirely sexual. This has been borne in mind while preparing the present paper where we directly analyse the two most important factors determining the maintenance of any polymorphism: inheritance and fitness effects. There are few reports of pericentric inversion inheritance in natural populations (Viseras & Camacho, 1991), but SCSs have been profusely studied and appear to show a frequent tendency to non-Mendelian transmission (Rhoades, 1942; Wilby & Parker, 1988; López-León *et al*., 1992). Here we analyse the inheritance and fitness effects of both types of polymorphism in *M. comosum*, grown in an experimental plot simulating field conditions.

Materials and methods

The present work was carried out in an experimental population of 71 bulbs of *Muscari comosum* that were randomly planted in an experimental plot in the autumn of 1994. Karyotypes for the pericentric inversion and the SCS were previously known: 38 (+/+), 18 (+/i), 11 (i/i), two (+/+l), one (+/il) and one (i/il), where + indicates the standard submetacentric chromosome, i indicates the acrocentric chromosome produced by pericentric inversion, and +l or il indicate the presence of a SCS in the long arm of chromosomes + or i, respectively (for details, see figs 1–4 in Ruiz Rejón & Oliver, 1981 and fig. 2 in Ruiz Rejón *et al*., 1987).

The bulbs, originally collected in Lluvi (Mallorca, Spain), were planted at random in a plot of 7 × 4 m. The plot was located far from natural populations of the species so that it would constitute a closed population where panmixis is possible. In the spring of 1995, the plants were allowed to reproduce naturally and their offspring were collected individually. For each plant, bulb weight, number of fruit, number of seeds and seed weight were recorded. In the autumn of 1995, all seeds obtained from each of 28 bulbs were sown to calculate germination ratio. For transmission studies, the karyotype of seeds from 17 bulbs was analysed by squashing roots in 2% acetic orcein.

Transmission analysis for each polymorphism was performed as follows. In homozygous bulbs, the null hypothesis (H_0) was that they produced heterozygous seeds at a frequency predicted by random fertilization with pollen from the 71 bulbs present in the experimental population. In heterozygous bulbs, however, inheritance was analysed by means of three statistical tests similar to those proposed by Perfectti & Pascual (1996) for controlled crosses. The first test (χ^2_{g}) reveals whether the two chromosomes appear in the seeds at the frequencies predicted by Mendelian segregation in the heterozygous bulbs following random pollination from the 71 bulbs (H_0). When the H_0 is rejected, this test may indicate the existence of meiotic drive on the female side, pollen selection and/or zygotic selection in seeds. The second test (χ^2_{z}) includes the same assumptions as the first, but analyses karyotypic frequencies in the seed progeny, H_0 being that these frequencies are consistent with those expected under female Mendelian segregation and random pollen usage. When significant, this test suggests the existence of zygotic selection, assortative mating or assortative fertilization. The third test (χ^2_{h}) analyses whether half of the offspring are heterozygotes (H_0), and generically provides information on whether segregation is Mendelian in at least one sex. For the present data, however, this test indicated specifically whether transmission was Mendelian through the female side of heterozygous bulbs. That is, we did not analyse controlled crosses, but rather mother-offspring where male parents were unknown and could be multiple, so that the H_0 has to assume a random sample of pollen from all 71 bulbs present in the experimental population. Thus, except if the expected pollen frequency were close to 1:1, 50% of heterozygous seeds can be yielded only through Mendelian segregation on the female side. For the two types of polymorphism analysed, the expected pollen frequencies were rather far from 1:1 (0.697/0.303 for +/i chromosomes in the inversion and 0.972/0.028 for +/l chromosomes in the SCS). Thus, in the present analysis, 50% heterozygous seeds are expected from Mendelian segregation on the female side. The possibility still remains that a 50% frequency of heterozygous seeds might be derived from female transmission bias compensating frequency differences in the random pollen sample. For instance, a 0.4+/0.6i sample of egg cells (resulting from inversion drive) fertilized by a random pollen sample (0.7+/0.3i) would yield offspring with a slight excess of heterozygotes (0.54). But this excess is directly dependent on the magnitude of drive for the i chromosome (e.g. 0.62 for drive equal to 0.8). This indicates that the most parsimonious hypothesis is to assume that 50% heterozygotes is not likely from Mendelian segregation through the female, because the corresponding test will only be weak for low drive values. In the case of the SCS, where pollen frequencies were much more biased from 0.5 (see above), the possibility of a compensating effect is even more unrealistic.

For the statistical analysis of effects on life-history traits, our first step was to investigate whether each variable was normally distributed, by means of the Shapiro–Wilk's test. Because only bulb weight fitted a normal distribution, nonparametric tests were applied in all cases. All statistical tests were carried out using BMPD statistical software (Dixon, 1990).

Results

Inheritance analyses

Table 1 shows very high heterogeneity in pollen fertilization success between homozygous bulbs, with an average excess of ++ seedlings when the bulbs were ++ and ii seeds when they were ii. The analysis of heterozygous bulbs (Table 2) showed that these bulbs yielded about half heterozygous seeds, implying that the + and i chromosomes were transmitted at the Mendelian ratio on the female side (χ^2_h

Table 1 Inheritance analysis of a pericentric inversion in *Muscari comosum* in homozygous bulbs. The null hypothesis was that they received a random sample of pollen from the whole population, so that each homozygote is expected to produce a frequency of heterozygous seeds equal to the population frequency of the chromosome it does not carry

		Observed seeds			Expected seeds				
Karyotype	Bulb no.	Homozygous	Heterozygous	Proportion of heterozygotes	Homozygous	Heterozygous	Proportion of heterozygotes	χ^2_1	*P*
++	3	8	9	0.529	11.85	5.15	0.303	4.13	0.042
	8	78	9	0.103	60.64	26.36	0.303	16.40	<0.001
	15	47	6	0.113	36.94	16.06	0.303	9.04	0.003
	17	41	33	0.446	51.58	22.42	0.303	7.16	0.007
	25	83	20	0.194	71.79	31.21	0.303	5.78	0.016
	47	33	21	0.389	37.64	16.36	0.303	1.89	0.169
	64	24	9	0.273	23.00	10.00	0.303	0.14	0.708
	Total	314	107	0.254	293.44	127.56	0.303	44.54	<0.001
$\chi^2_{\text{heterog.}} = 39.79$, d.f. = 6, $P<0.001$; $\chi^2_{\text{accumul.}} = 4.75$, d.f. = 1, $P = 0.029$									
ii	13	13	36	0.735	14.85	34.15	0.697	0.33	0.566
	22	42	27	0.391	20.91	48.09	0.697	30.52	<0.001
	23	18	26	0.591	13.33	30.67	0.697	2.35	0.125
	29	13	29	0.690	12.73	29.27	0.697	0.01	0.920
	33	3	14	0.824	5.15	11.85	0.697	1.29	0.256
	Total	89	132	0.597	66.96	154.04	0.697	34.50	<0.001
$\chi^2_{\text{heterog.}} = 24.09$, d.f. = 4, $P<0.001$; $\chi^2_{\text{accumul.}} = 10.41$, d.f. = 1, $P = 0.001$									

Table 2 Inheritance analysis of a pericentric inversion in *Muscari comosum* in heterozygous bulbs (+i)

	Observed			χ^2_g			χ^2_z			χ^2_h		
Bulb no.	++	+i	ii	χ^2	*P*	*P′*	χ^2	*P*	*P′*	χ^2	*P*	*P′*
5	16	26	10	0.74	0.390	NS	0.82	0.664	NS	0.00	1.000	NS
6	14	24	7	0.17	0.680	NS	0.28	0.867	NS	0.20	0.655	NS
16	10	12	6	0.18	0.671	NS	1.02	0.600	NS	0.57	0.450	NS
30	13	30	20	12.53	0.0004	0.0016	15.18	0.0005	0.002	0.14	0.708	NS
36	34	72	13	0.11	0.740	NS	5.38	0.068	NS	5.25	0.022	NS

P′, probability corrected by the sequential Bonferroni method.

was nonsignificant in the five cases). Bulb no. 30, however, yielded a significant excess of ii seeds.

With respect to the SCS, Table 3 shows that bulbs carrying both chromosomes lacking the SCS, received a random sample of pollen. The heterozygous bulbs, however, produced a highly significant excess of heterozygous seeds, in most cases paralleled by a significant increase in the frequency of l chromosomes transmitted (Table 4).

Effects on fitness

Forty-six bulbs were used to analyse possible fitness effects of both polymorphisms: 19 bulbs were + +, 14 bulbs were +i, nine bulbs were ii, two bulbs were +/+l (bulbs nos 47 and 64), one bulb was +/il (bulb no. 30) and one bulb was i/il (bulb no. 33). Four fitness-related life-history traits were recorded: bulb weight, number of fruits, number of seeds and seed weight. Three additional variables were obtained by combination of these four: the mean number of seeds per fruit, the absolute investment of a bulb in seed production (calculated as the product of the number of seeds and the mean weight per seed) and the relative investment in seeds (calculated as the absolute investment in seeds divided by bulb weight).

Nonparametric Spearman rank correlation analyses of the variables measured showed a significant trend for large bulbs to yield larger seeds ($r_s = 0.532$, $N = 46$, $t = 4.17$, $P = 0.00014$), but no significant correlation was found between bulb size

Table 3 Analysis of pollen usage by *Muscari comosum* bulbs lacking a supernumerary chromosome segment (SCS). The null hypothesis was that they received a random sample of pollen from the whole population, so that each + + bulb is expected to produce a frequency of heterozygous seeds (+l) equal to the frequency of the SCS in the population (0.028)

	Observed seeds			Expected seeds				
Bulb no.	+ +	+l	Proportion +l	+ +	+l	Proportion +l	χ^2_1	P
3	17	0	0	16.52	0.48	0.028	0.49	0.484
5	48	3	0.059	49.56	1.44	0.028	1.75	0.186
6	44	1	0.022	43.73	1.27	0.028	0.06	0.806
8	85	2	0.023	84.55	2.45	0.028	0.08	0.777
13	47	2	0.041	47.62	1.38	0.028	0.29	0.590
15	52	1	0.019	51.51	1.49	0.028	0.17	0.680
16	26	2	0.071	27.21	0.79	0.028	1.91	0.167
17	73	1	0.014	71.92	2.08	0.028	0.58	0.446
22	68	1	0.014	67.06	1.94	0.028	0.47	0.493
23	43	1	0.023	42.76	1.24	0.028	0.05	0.823
25	101	2	0.019	100.10	2.90	0.028	0.29	0.590
29	42	0	0	40.82	1.18	0.028	1.22	0.269
36	114	5	0.042	115.65	3.35	0.028	0.83	0.362
Total	760	21	0.027	759.00	22.00	0.028	8.19	0.831

$\chi^2_{\text{heterog.}} = 8.14$, d.f. = 12, $P = 0.774$; $\chi^2_{\text{accumul.}} = 0.05$, d.f. = 1, $P = 0.823$

Table 4 Inheritance analysis of a SCS in *Muscari comosum* in heterozygous bulbs

	Observed			χ^2_g			χ^2_h		
Bulb no.	+ +	+l	ll	χ^2	P	P'	χ^2	P	P'
30	17	46	1	6.63	0.010	0.030	13.35	0.00026	0.00078
33	3	14	0	3.78	0.052	NS	7.12	0.008	0.016
47	5	49	0	20.01	0.000008	0.000032	35.85	<0.00001	<0.00004
64	11	22	0	1.64	0.200	NS	3.67	0.055	NS

P' = Probability corrected by the sequential Bonferroni method. Because of the extremely low frequency of the ll bulbs, the χ^2_g and the χ^2_z tests are practically equivalent and the number of fruits, number of seeds, seeds per fruit or absolute investment in seeds (data not shown). Likewise, the number of fruits did not correlate with seed weight or the number of seeds per fruit. Finally, no significant correlation was found between seed weight and the number of seeds.

Table 5 shows that the two karyotypes carrying the pericentric inversion (+i and ii) had a bulb weight significantly higher than ++ individuals. The remaining traits did not differ significantly between karyotypes. Values for all traits, being closely similar between the two karyotypes carrying the inversion, were pooled for subsequent analyses. Mann–Whitney tests confirmed that the pericentric inversion affected bulb weight ($z = 3.12$, $P = 0.0126$ after correction by the sequential Bonferroni method) but not the remaining traits. Contrast of variances showed that variance in the relative seed investment was significantly greater in bulbs carrying the inversion ($F_{20,24} = 5.63$, $P = 0.0007$ after correction by the sequential Bonferroni method) (see SE values in Table 5), but no other trait was affected. Similar analyses showed no effect of the SCS on any of the variables shown in Table 5, at both mean and variance levels.

Finally, the three karyotypes differing for the pericentric inversion did not show significant differences in germination rate (75.29% for ++, 81.89% for +i and 82.18% for ii; Kruskal–Wallis ANOVA: $H = 1.85$, $N = 28$, $P = 0.40$). The SCS also had no effect on germination rate (Mann–Whitney test: $z = 0.68$, $P = 0.49$).

Discussion

Our results provide new insights into several aspects of the inheritance and fitness of both a pericentric inversion and a SCS located in the second chromosome pair of *M. comosum*. With respect to the inheritance of the inversion, some homozygous bulbs (either with or without inversion) showed nonrandom pollination. As is apparent in Table 1, the homozygous standard bulbs (++) showing nonrandom pollination yielded an excess of homozygous standard seedlings, and the homozygous bulbs for the inversion (ii) with nonrandom pollination produced an excess of homozygous seedlings for the inversion. The most likely explanation is the existence of a certain rate of self-pollination. In this respect, it has been demonstrated by isozyme analyses that the reproductive biology of *M. comosum* tends towards cross-pollination (Ruiz Rejón *et al*., 1982, 1985). However, its floral characteristics do not rule out the possibility of a certain rate of self-pollination (Knoll, 1921); in this regard Bentzer (1973) found some seed-setting after spontaneous selfing in this species.

As a whole, Table 2 indicates that the majority of bulbs heterozygous for the inversion (+i) showed Mendelian ratios on the female side and random pollination, with the exception of bulb no. 30. As this bulb was doubly heterozygous (++/il), the excess of ii seeds was most likely a consequence of hitch-hiking caused by the accumulation of the SCS. In fact this bulb yielded 13 (++/++), four (++/i+), 26 (++/il) and 20 (i+/il) seeds. Therefore, it produced 46 seeds (73% of total progeny) carrying an il chromosome most probably inherited from the mother. The high tendency for the transmission of the il chromosome, as a whole, through the mother is explained by the fact that both the inversion and the SCS suppress chiasma formation (Ruiz-Rejón *et al*., 1987). The high transmission rate of the inversion in this bulb was thus a passive

Table 5 Comparison of seven fitness-related traits between the three karyotypes for the inversion, by means of the Kruskal–Wallis nonparametric ANOVA

	++ ($N = 21$)		+i ($N = 15$)		ii ($N = 10$)		Kruskal–Wallis ANOVA		
Item	Mean	SE	Mean	SE	Mean	SE	H	P	P'
Bulb weight	4.55	0.42	6.70	0.71	6.54	0.44	9.857	0.0072	0.050
Number of fruits	36.29	4.19	26.00	3.76	27.10	4.85	3.135	0.2085	NS
Number of seeds	141.00	19.07	105.33	19.93	100.90	23.10	2.707	0.2584	NS
Mean seed weight	6.50	0.53	7.00	0.32	7.89	0.67	5.017	0.0814	NS
Seeds per fruit	4.01	0.35	3.94	0.32	3.41	0.33	1.298	0.5225	NS
Absolute investment in seeds	852.55	121.26	754.69	146.50	785.53	172.55	0.421	0.8103	NS
Relative investment in seeds	231.27	44.33	122.71	25.24	114.84	21.49	6.178	0.0456	NS

P', probability corrected by the sequential Bonferroni method.

consequence of SCS accumulation. The absence of significance for the χ^2-test in Table 2 for this bulb is not a consequence of a Mendelian segregation ratio through the mother (which would run against the accumulation of the il chromosome). In this case, the 50% of seeds heterozygous for the inversion is simply the result of random fertilization of two types of egg cells with frequencies biased in favour of the il type (0.27 + +: 0.73 il) by two types of pollen with frequencies (0.62 + +: 0.38 +i), which are those expected from a random pollen sample from the 71 bulbs in the experimental population.

These results indicate that the pericentric inversion in *M. comosum* shows Mendelian transmission through both the paternal and maternal lines, but also suggest that linkage to the SCS (hitch-hiking) could give the inversion some transmission advantage. In other words, the il chromosome was transmitted with a higher efficiency than the +l chromosome in double heterozygotes. This possibility remains to be tested in future work where double heterozygotes in coupling and repulsion phases can be analysed for transmission.

It is surprising that although pericentric inversion polymorphisms have been frequently reported in a wide variety of organisms (White, 1973; Watanabe & Noda, 1974), the transmission of the standard and inverted chromosomes has rarely been analysed, even though this is one of the main factors determining the maintenance of polymorphism. The only known case was reported by Viseras & Camacho (1991) in the grasshopper *Aiolopus strepens*, where a gravid female collected in the field transmitted the standard and the inverted chromosome at about the same rate. Our present data point to the same result, suggesting that pericentric inversions do not seem to show drive, but more cases need to be analysed before a firm conclusion can be reached.

Analysis of seedlings from bulbs lacking the SCS showed that they received a random sample of pollen with respect to the SCS (Table 3). However, three out of the four bulbs heterozygous for the SCS produced a significant excess of heterozygous seedlings (Table 4). This non-Mendelian transmission most likely results from an accumulation mechanism on the female side involving preferential segregation of the l chromosome to the egg cell in heterozygotes. From the sum of karyotypic frequencies in the seeds of the four heterozygous bulbs (36 + +, 131 +l, 1 ll) and assuming random pollen fertilization (the + chromosome at a frequency of 0.972 and the l at a frequency of 0.028), we can calculate the transmission ratio of the l chromosome (k_l): frequency of heterozygotes $= 0.972 \times k_l + 0.028 \times (1 - k_l)$, so that $131/(36+131+1) = 0.972 \times k_l + 0.028 - 0.028\,k_l$; $k_l = (0.78 - 0.028)/(0.972 - 0.028) = 0.796$. The average transmission ratio for the l chromosome is thus about 0.8, which implies a powerful accumulation mechanism favouring the increase in frequency of the SCS in this population.

It is common to find that SCSs display accumulation mechanisms. Examples have been reported in plants such as maize (Rhoades, 1942), *Tulipa australis* (Ruiz Rejón *et al.*, 1988), *Rumex acetosa* (Wilby & Parker, 1988), or at the tetraploid level of *Scilla autumnalis* (Ainsworth *et al.* 1983), and animals like the grasshopper *Chorthippus jacobsi* (in the S_8 chromosome; López-León *et al.*, 1992). Other SCSs, however, reveal Mendelian transmission, as in the cases of *Scilla autumnalis* at the diploid level (Jamilena *et al.*, 1995) or the grasshopper *Chorthippus jacobsi* (M_5 and M_6 chromosomes; López-León *et al.*, 1992) and the locust *Locusta migratoria* (Pardo *et al.*, 1993), and there is even a case in the grasshopper *Eyprepocnemis plorans* where the SCS is undertransmitted through heterozygous females carrying B chromosomes (López-León *et al.*, 1991, 1994). Thus, SCSs constitute excellent material for investigating accumulation mechanisms.

The absence of phenotypic correlation between seed weight and seed number indicates the absence of an offspring size-to-number trade-off. This may be because the experimental population experienced more benign conditions than most natural populations. In another lily plant, *Scilla autumnalis*, however, we also failed to find this trade-off in a natural population (Jamilena *et al.*, 1995). This might be a general characteristic of bulbous plants, because the bulb may provide sufficient nutrients for the plant to avoid resource limitation during reproduction.

Our results have shown that the different karyotypes for the two types of chromosomal polymorphism in the second chromosome pair of *M. comosum* displayed similar values for several life-history traits related to female fitness, such as number of fruits, number of seeds and seed weight. However, those plants carrying the inversion had heavier bulbs than those lacking it (Table 5), and a greater variance in the relative seed investment. In addition, plants carrying the inverted chromosome showed a significant trend towards a lower relative investment in seeds, although significance was lost after Bonferroni application (Table 5). This suggests that inversion carriers may benefit by having heavier bulbs that allocate relatively less energy to reproduction, thus reserving more resources for other functions. If variation for relative investment in seeds involves additive genetic variation, then natural selection could favour the pericentric inversion. Because relative seed investment was similar for +i and ii individuals (Table 5), and other factors being equal, this process should lead to the fixation of the inverted chromosome. Calculation of heritability and analysis of the frequency of standard and inverted chromosomes in natural populations, over several years, will clarify the details of the maintenance of this polymorphism. For the moment, we know that it is not maintained by intragenomic selection, because it does not show drive, and it may be maintained through the action of phenotypic selection, which would not be surprising given the intimate relationship between inversions and supergenes (Prakash & Lewontin, 1968).

The SCS, however, is clearly maintained by powerful drive on the female side. This suggests its selfish nature, the same as that of other SCSs showing drive. We have not detected any effect on fitness, although this result should be considered preliminary because only four bulbs carrying the SCS could be analysed.

It is clear that SCSs can be maintained in natural populations only by showing drive or else by exerting some beneficial effect on carriers. The first applies to the case of *M. comosum* (the present study) and the second to the case of *Scilla autumnalis*, where transmission is Mendelian but SCS presence (mainly in heterozygotes) results in heavier seeds (Jamilena *et al*., 1995). There is even one species where both mechanisms seem to take place. *Tulipa australis* shows drive for the SCS and a higher germination rate for heterozygous seeds (Ruiz Rejón *et al*., 1988). The SCS in *M. comosum* could thus be considered a selfish element, that in *S. autumnalis* a heterotic one, and that in *T. australis* a strange case where a selfish element has evolved to benefit carriers.

An additional interesting question is why the SCS in *M. comosum* displays a low frequency in natural populations despite showing such high drive and not being detrimental to carrier fitness. A possible answer is a recent origin of the SCS, but this possibility is not supported by its presence in most populations analysed (Ruiz Rejón *et al*., 1990). In addition, the euchromatic nature of the SCS suggests, under the hypothesis by Camacho & Cabrero (1987), that it could actually be a relic of a chromosome segment that formed part of the standard genome but underwent a tolerated deletion, and thus now is in the last stage of a process leading to its disappearance. If this is correct, then it might have gained accumulation in Mallorca, a property absent from most of the remaining populations. Testing this hypothesis would require inheritance analyses in populations where SCS frequency is low. If true, it would explain why the SCS was so frequent in two populations analysed from this island but so rare in the remaining populations. It is also remarkable that two populations collected at Menorca, a nearby island, lacked the SCS, which suggests the high importance of genetic drift, in general, and founder effects, in particular, in making up SCS frequency in natural populations.

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