Theor Appl Genet (1999) 98: 557–563

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Morphological and RAPD markers show a highly skewed distribution in a pair of reciprocal crosses between hemisexual dogrose species, *Rosa* sect. *Caninae*

Received: 25 June 1998 / Accepted: 28 July 1998

Abstract The dogroses, *Rosa* sect. *Caninae*, are polyploid and characterized by their unique meiosis with an unequal number of chromosomes in the male and female gametes. The pollen cells have 7 chromosomes and the egg cells 21, 28 or 35 depending on the ploidy level of the species. The resulting matroclinal inheritance was studied with both morphological and molecular markers in a pair of reciprocal crosses between *R. dumalis* and *R. rubiginosa* (2n = 35). A canonical discriminant analysis based on seven morphological characters showed only a minor overlapping between the two progeny groups. In addition, the *R. dumalis* × *R. rubiginosa* offspring were more heterogeneous than the offspring from the reciprocal cross in each of the characters analysed. Eleven RAPD markers specific for the *R. dumalis* parent and 10 RAPD markers specific for the *R. rubiginosa* parent were scored in the offspring. Each of the offspring exhibited either all, or all-but-one, of the seed parent markers. The average number of pollen donor markers found in the offspring was 3.2 (*R. dumalis* × *R. rubiginosa*) and 2.7 (*R. rubiginosa* × *R. dumalis*). About half of the pollen donor markers were never transmitted to the progeny. This is, to our knowledge, the first time the highly skewed chromosome distribution in *Rosa* sect. *Caninae* has been demonstrated with statistically evaluated morphological data and with molecular markers.

Key words *Rosa* sect. *Caninae* · Biometrics · Heterogamy · RAPD · Segregation distortion

Communicated by P. M. A. Tigerstedt

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Introduction

An extremely unusual mode of meiotic chromosome distribution was described in the dogroses, *Rosa* sect. *Caninae* L., at the beginning of this century (Täckholm 1920; Blackburn and Heslop-Harrison 1921). All dogrose species are polyploid (x = 7) with 28, 35 (most common) or 42 chromosomes. Only 7 bivalents form at meiosis and the remainder of the chromosomes occur as univalents. The egg cells contain 7 chromosomes from the bivalent formation plus all the univalents, whereas viable pollen grains have only the 7 chromosomes from the bivalents.

Taxonomic treatments of the dogroses have sometimes resulted in the kind of nomenclatural proliferation encountered in many apomictic plant groups (Almquist 1919). Although still controversial, modern classifications usually recognize only about 20–30 dogrose species (Zielinski 1985). These occur mainly in Europe, but also in North Africa and northwestern Asia. The dogroses are perennial thorny shrubs, growing in disturbed habitats such as roadsides and open pastures. Dogroses are self-compatible (Jicinska 1976a) but outcrossing and hybridization is common (Cole and Melton 1985).

Grant (1971) described the reproductive system in sect. *Caninae* as 'permanent odd polyploidi', and this type of reproductive system is very rare in plants. A somewhat similar type of reproductive system is found in *Leucopogon juniperus* (Epacridaceae) with 2n = 3x = 12 chromosomes, where four bivalents and four univalents are formed at meiosis (Smith-White 1955). Another example is *Andropogon ternatus* (Poaceae) with 2n = 3x = 30 chromosomes. Viable pollen cells contain 20 chromosomes, 10 from the bivalent formation and 10 from the univalents, whereas egg cells contain only the 10 chromosomes from the bivalents (Norrmann and Quarin 1987).

The unequal segregation of meiotic chromosomes is expected to result in a skewed distribution of inherited

characteristics. In keeping with this, interspecific reciprocal crosses both within sect. *Caninae* and between *Caninae* and other *Rosa* sections have shown a marked difference in morphology between progeny groups, depending on which species acted as the seed parent (Gustafsson 1944). Although these results were not analysed statistically, they gave the impression that properties from the seed parent always predominated. A pronounced morphological influence from the seed parent has also been mentioned in several other papers (Rowley 1967; Kroon and Zeilinga 1974; Melville 1975; Graham and Primavesi 1993). In contrast, Jicinska (1976b) reports intermediate inheritance for some characters.

Whereas morphological markers are cheap and easy to use, they are also very sensitive to environmental influences and to the developmental stage of the plant. Moreover, as a result of dominance effects, morphological markers may be poorly suited to progeny analyses. In the last two decades, molecular markers, such as RFLPs (restriction fragment length polymorphism) and RAPDs (random amplified polymorphic DNA), have become increasingly important in the genetic analyses of plants. Both types of markers have been successfully used in identifying rose cultivars as well as wild rose species and in the study of genetic relationships among cultivars and species (Hubbard et al. 1992; Torres et al. 1993; Ben-Meir and Vainstein 1994; Vainstein and Ben-Meir 1994; Debener et al. 1996; Gallego and Martinez 1996; Millan et al. 1996). Debener et al. (1997) were the first to use molecular markers on controlled interspecific crosses within *R.* sect. *Caninae*, but did not mention the *Canina* meiosis or its expected effects on the marker distribution.

We are in a situation where a unique chromosomal distribution was described almost 80 years ago on the basis of cytological evidence – but where no serious attempt has ever been made to analyse this distribution with quantifiable marker data. The investigation described here was therefore undertaken on a pair of reciprocal crosses between two dogrose species, *R. dumalis* Bechst. and *R. rubiginosa* L. (both 2n = 35), to quantify the inheritance of morphological and molecular markers within the two progeny groups.

Material and methods

Plant material

The cross *R. dumalis* subsp. *dumalis* × *R. rubiginosa* and its reciprocal were made in 1992. One plant from each species was used as both seed and pollen parent, respectively. The *R. dumalis* plant had been obtained from Tjörnedala and the *R. rubiginosa* plant from Fjälkestad, both in S Sweden. The resulting seedlings were planted in adjacent rows in an experimental field in 1993. Morphological measurements were made in 1996, and newly developed leaves from the two parental plants and the progenies were collected and stored in −80°C for DNA extractions.

Morphological measurements

The choice of morphological characters was based on previous investigations where the same characters had proved useful for species discrimination (Nybom et al. 1996, 1997). When the plants were in full bloom, three flowers (preferably the apical flower in three different inflorescences) were collected from each plant. In the field we measured: (1) length and (2) width of the ovary. The petals were removed, and the remainder brought into the laboratory and photocopied. On the photocopies we measured (3) length and (4) width of one of the sepals on each flower, avoiding the largest and the smallest sepal, and (5) total amount of sepal serration on each flower. We also noted (6) on which day each plant reached peak flowering. *Rosa dumalis* flowers before *R. rubiginosa*, but there is some overlapping. The day on which the first plants reached peak flowering was denoted as 1, with the following days numbered consecutively until all plants had flowered. We analysed 37 plants of *R. dumalis* × *R. rubiginosa* and 45 plants of *R. rubiginosa* × *R. dumalis*. In August, the largest leaf was collected from three shoots on each plant. The leaves were pressed and (7) the quotient length/width was measured on a subapical leaflet.

We used the mean of the three measurements of each character from each plant, and the day of peak flowering in the statistical analyses. Because of leaf deformation (caused by powdery mildew), especially on *R. dumalis* × *R. rubiginosa*, only 30 plants of *R. dumalis* × *R. rubiginosa* and 40 plants of *R. rubiginosa* × *R. dumalis* were available for the leaf measurements.

Statistical analyses

The SPSS Data Analysis Package (Norusis 1990a,b) was used for the calculations. A set of univariate analyses of variance were performed for each morphological character with the two progenies as a group variable, and coefficients of variation were calculated. A multivariate analysis, canonical discriminant analysis, was then performed with all seven characters entered simultaneously. A subsequent classification test was carried out, in which the individual plants were reassigned to the two groups defined by the discriminant function: the higher the percentage of correctly placed plants, the more well-defined are the progeny groups.

DNA extractions and RAPD analysis

DNA was extracted according to Holm (1995) and stored in 1 × TE solution at +4°C. Amplifications were carried out in a 25 µl reaction mixture containing 2.5 m*M* $MgCl_2$ (Advanced Biotechnologies), 0.5 µ*M* primer (Operon Technologies), 1 × buffer solution no. 4

Table 1 RAPD primers and analysed bands specific for the parents *R. dumalis* and *R. rubiginosa*

Primer ID	Sequence	Number of bands analysed	
		R. dumalis	*R. rubiginosa*
OPA-16	AGCCAGCGAA	1	2
OPB-07	GGTGACGCAG	2	2
OPE-09	CTTCACCCGA	1	2
OPE-11	GAGTCTCAGG	2	0
OPE-13	CCCGATTCGG	2	1
OPE-19	ACGGCGTATG	1	0
OPF-06	GGGAATTCGG	0	1
OPG-01	CTACGGAGGA	1	1
OPG-12	CAGCTCACGA	1	1
Total		11	10

(Advanced Biotechnologies), 0.2 m*M* nucleotide mix (Boehringer and Mannheim), approximately 30 ng genomic DNA and 1 U *Taq* polymerase (Advanced Biotechnologies). The mixture was overlaid with 25 µl mineral oil (Perkin Elmer). After an initial denaturation at 94°C for 5 min in a Hybaid Omnigene Thermocycler, the reaction mixture was subjected to amplification for 40 cycles of 1 min at 94°C, 1 min at 36°C and 2 min at 72°C followed by a 7-min extension time at 72°C. The fragments were separated on a 1.8% agarose gel containing ethidium bromide and using TPE buffer. The parental plants and a molecular-weight marker (Boehringer and Mannheim MWM VI) were present at four places on each gel. The gel was photographed under UV light. A total of 38 plants of *R. dumalis* × *R. rubiginosa* and 40 plants of *R. rubiginosa* × *R. dumalis* was analysed.

One hundred primers were tested for amplification of bands that could differentiate between the two parental plants; 11 of these did not amplify any DNA fragments at all. Of the remaining 89 primers, 9 which gave unambiguous and reproducible polymorphic bands were subsequently used for both progeny groups (Table 1). Each of these 9 primers produced 1–4 polymorphic bands. A total of 21 polymorphic bands was scored: 11 specific for *R. dumalis* and 10 specific for *R. rubiginosa*.

Results

Morphology

The two progeny groups could be distinguished already on superficial observations since each plant closely resembled its respective seed parent, *R. dumalis* or *R. rubiginosa*.

Four of the seven morphological characters showed significant differences between the two progeny groups: sepal length, sepal serration, peak flowering and leaflet length/width quotient (Table 2). The coefficients of variation for each character showed the progeny group *R. dumalis* × *R. rubiginosa* (i.e. with *R. dumalis* as seed parent) to be more variable than the progeny group from the reciprocal cross with, in particular, peak flowering being quite extended. The two groups were also well separated by the discriminant analysis (Fig. 1). The canonical correlation, which represents the total variance attributable to differences among the groups, was 0.755, and the group centroids were −1.310 and 0.984, respectively. The subsequent classification test reassigned 90% of the 70 plants into the correct progeny groups.

RAPD analysis

Clear and easily scored band patterns were obtained, and the consistency between repeated amplifications was very high (Fig. 2). Ten of the 11 *R. dumalis* specific markers were found in all 38 *R. dumalis* × *R. rubiginosa* offspring, whereas the 11th marker was found in only 7 offspring (Fig. 3). Of the 10 markers for the pollen donor in this cross, i.e. *R. rubiginosa*-specific bands, only 5 markers were transmitted and these appeared in 33, 32, 31, 23 and 3 offspring, respectively. On an

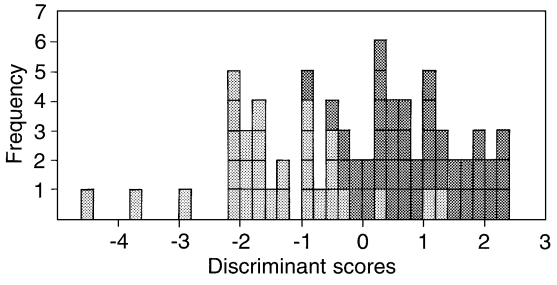

Fig. 1 Discriminant analysis calculated on seven morphological characters for discrimination between a pair of reciprocal crosses. ▨ *R. dumalis* × *R. rubiginosa*, ▩ *R. rubiginosa* × *R. dumalis*

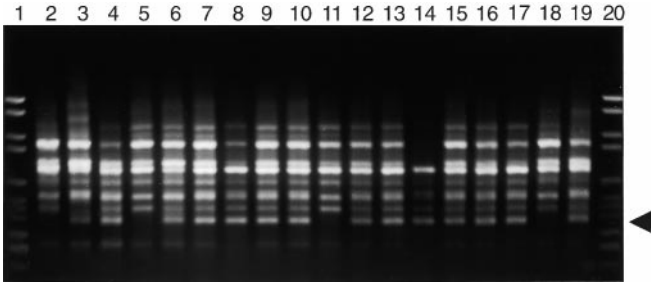

Fig. 2 RAPD bands produced by primer F-06. From *left* to *right*: *lane 1* molecular-weight marker no. IV (Boehringer and Mannheim), *2 R. dumalis*, *3 R. rubiginosa*, *4–17 R. dumalis* × *R. rubiginosa*, *18 R. dumalis*, *19 R. rubiginosa*, *20* molecular-weight marker no. IV. *Arrow* indicates polymorphic band

Table 2 Mean, standard deviation (SD) and coefficient of variance (CV) for the two crosses *R. dumalis* × *R. rubiginosa* and *R. rubiginosa* × *R. dumalis*, and one-way analysis of variance performed for variation between the two progeny groups, with *F* values, degrees of freedom (*df*) and *P* values

Characters	*R. dumalis* × *R. rubiginosa*			*R. rubiginosa* × *R. dumalis*			*F*	*df*	*P*
	Mean	SD	CV	Mean	SD	CV			
Ovary length	8.918	0.655	7.3	8.795	0.495	5.6	0.927	1/80	0.339
Ovary width	6.135	0.531	8.6	5.955	0.428	7.2	2.845	1/80	0.096
Sepal serration	11.586	2.459	21.2	13.743	1.852	13.5	20.222	1/80	0.000
Sepal length	24.468	2.916	11.9	25.735	2.020	7.8	5.291	1/80	0.024
Sepal width	4.405	0.403	9.1	4.371	0.340	7.8	0.172	1/80	0.680
Time of peak flowering	3.811	2.817	73.9	5.818	1.859	32.0	14.735	1/80	0.000
Leaflet quotient	1.685	0.098	5.8	1.586	0.071	4.5	24.149	1/68	0.000

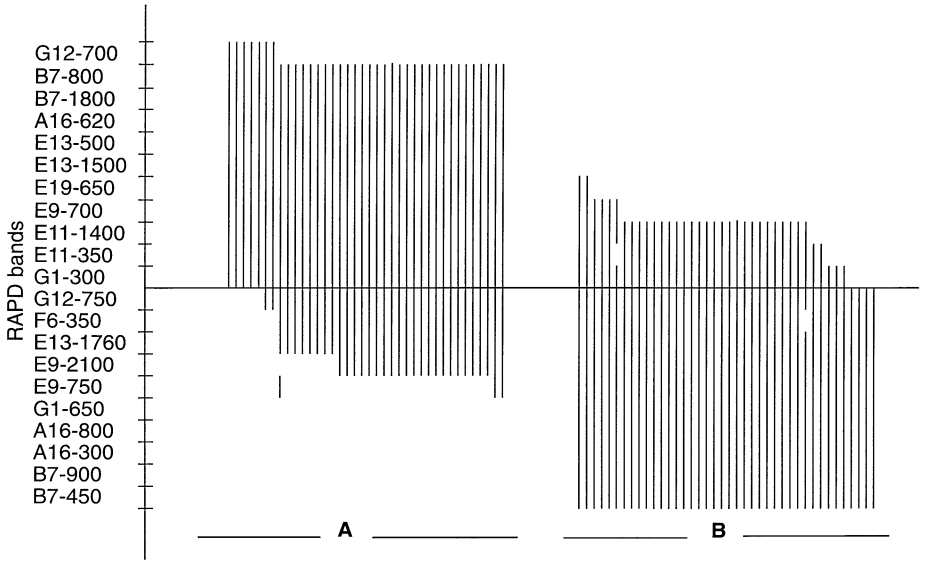

Fig. 3 Distribution of RAPD bands in the progenies. The bands above the horizontal line are specific for *R. dumalis* and the bands below the line are specific for *R. rubiginosa*. Each vertical line represents a progeny plant. A = *R. dumalis* × *R. rubiginosa*, B = *R. rubiginosa* × *R. dumalis*

average, each offspring inherited only 3.2 pollen donor markers.

Nine of the 10 *R. rubiginosa*-specific markers were found in all 40 *R. rubiginosa* × *R. dumalis* offspring, and the tenth marker was found in 39 of them. Of the 11 pollen donor markers, in this cross *R. dumalis*-specific bands, again only 5 were transmitted. These markers were found in 36, 32, 32, 4 and 2 plants, respectively. In this cross, the offspring inherited an average of 2.7 pollen specific markers.

Five plants from the *R. dumalis* × *R. rubiginosa* cross and 4 from the reciprocal cross, inherited all the seed parent markers but none of the pollen donor markers.

RAPD bands are dominantly inherited, and it is almost impossible to separate homozygotes from heterozygotes on the basis of band intensity. Nevertheless, the parents must have been heterozygous for all our markers since none of the markers were transmitted to all offspring, i.e. the markers may occur in one to four of the genomes but not in all five. Disomic inheritance of a heterozygous marker, occurring in one parent, is expected to result in a 1:1 ratio. Goodness-of-fit tests, calculated on both progeny groups taken together, showed that all markers deviated significantly from a 1:1 ratio, with $P<0.001$. This is not surprising, since four of the five genomes in the offspring are inherited from the maternal parent. Still a 1:1 ratio could be expected for paternally inherited markers, provided that, in a given plant, the same two genomes are always involved in bivalent formation, and that the markers occur in one of these two genomes but not in both. Goodness-of-fit tests were therefore calculated on the distribution of pollen donor markers for each of the progeny groups. All but one pollen donor marker still deviated significantly from a 1:1 ratio (one with $P<0.05$, two with $P<0.01$ and the remainder with $P<0.001$). Instead of being found in a 1:1 ratio, pollen markers appear to fall into two classes, those that occur in most of the offspring and those that occur in very few or no offspring.

Discussion

Matroclinal inheritance

Several factors, apart from a skewed chromosomal distribution, may result in more or less matroclinal offspring. The seed parent may, for example, influence its offspring through the endosperm which contains more maternal material than paternal, through cytoplasmic inheritance in the form of plastids and mitochondria, and through phenotypic effects mediated by environmental factors, such as stress, during seed development. These maternal effects are most pronounced in seed size and in young plants, and usually decrease in older plants (Roach and Wulff 1987). Also, they seldom cause any major deviation from the phenotype expected from Mendelian-inherited nuclear genes. The matroclinal progeny mentioned in several earlier dogrose studies is therefore likely to derive mainly from the aberrant chromosomal distribution (Gustafsson 1944; Rowley 1967; Kroon and Zeilinga 1974; Melville 1975; Graham and Primavesi 1993).

Lacking a comparable material for morphological analysis of the parental genotypes, we could not calculate the genetic distance between parents and progeny in our study. Nevertheless, the pronounced difference in morphological characteristics between the two progeny groups is highly suggestive of a strong matroclinal inheritance. Our results thus tie in with those of Gustafsson (1944) and Jicinska (1976b), who state that leaf characters are mainly matroclinally inherited when

plants from sect. *Caninae* are used as seed parents, and plants of *R. rugosa* Thunb. as pollen donors. Jicinska (1976b) added that prickles are patroclinally inherited and that flower and hip characters are intermediate between the parents. It should, however, be noted that no statistical data evaluation was reported in the above studies.

Discrimination between matroclinal and intermediate inheritance using morphological characters may, however, not be completely straightforward. In adult hybrid plants, morphological characters are usually a mosaic of parental and intermediate characters rather than just intermediate ones. Even in a single entity such as a leaf, different dominant genes lead to a mixture between parental features rather than an intermediary. The expression of intermediate versus parental characters also varies with the hybrid analysed (Melville 1960; Rieseberg and Ellstrand 1993). In a study using only leaf characters, hybrids between *R. rubiginosa* and *R. dumalis*, and between *R. rubiginosa* and *R. sherardii* Davies ($2n = 35$), were compared with seedlings derived from selfing and from intraspecific crosses (G. Werlemark, manuscript in preparation). A discriminant analysis showed that offspring resembled the pollen donor species in the cross *R. rubiginosa* × *R. dumalis*, whereas the opposite was true in the cross *R. rubiginosa* × *R. sherardii*.

Due to the above mentioned problems with morphological markers, we decided to also use RAPD markers in our study. The distribution of our RAPD markers is highly indicative of a pronounced matroclinal inheritance. The progeny plants inherited a mean of 10.1 seed parent markers as compared to only 2.9 pollen donor markers. Moreover, 9 plants appear to have inherited their markers exclusively from the seed parent.

Apomixis

An extreme form of matroclinal inheritance is obtained through apomixis, i.e. the ability to set seed without prior fertilization. In our material, apomixis cannot be excluded in those 9 offspring which inherited all the seed parent-specific RAPD markers and none of the pollen donor markers. However, considering the low number of pollen donor markers generally transmitted in our material, complete lack of pollen donor markers could perhaps result from random marker distribution. Accidental selfing can also not be completely ruled out. Nevertheless, the existence of some additional difference between plants with and without pollen donor markers (e.g. sexual versus apomictic derivation) was indicated by *t*-tests: in each of the two progeny groups, two of the morphological characters (sepal length and ovary width) separated plants with RAPD pollen donor markers from those lacking such markers.

The possible occurrence of apomixis in dogroses has been discussed in several papers. As early as 1920 Täckholm concluded from his cytological findings that, although 'numerous spontaneous hybrids' were discovered in nature, reproduction took place mainly through apomixis. Kroon and Zeilinga (1974), using so-called Edelcaninas (commercial rootstocks, sect. *Caninae*) as seed parents and pollen donors from different *Rosa* sections, reported that two-thirds of the offspring were hybrids and that 'the character of the seed parent mostly dominated in the hybrids', and one-third were of apomictic origin. The classification of the offspring was based on morphological and cytological analyses which were, however, not specified in detail. Wissemann and Hellwig (1997) reported that all taxa within sect. *Caninae* were able to produce seeds after emasculation, which was taken as an indication of apomixis. However, contrary to the high viability generally encountered in apomicts, the proportion of filled seeds following emasculation was only 5% of that encountered in seeds produced by xenogamy.

Other reports have questioned the occurrence of apomixis in dogroses. Gustafsson and Håkansson (1942) and Cole and Melton (1986) were not able to produce any seeds in their emasculation experiments, but this does not rule out the occurrence of pseudogamy (with pollination being necessary to trigger the parthenogenetic egg development). More importantly, Fagerlind (1940) did not find any unreduced embryo sacs in his embryological investigations in sect. *Caninae*.

Obviously the hemisexual mode of reproduction in dogroses leads to matroclinal offspring that can sometimes be rather difficult to discriminate from apomictically derived offspring. Therefore, we believe that many more markers are needed before making any inferences about whether apomixis occurs in *R.* sect. *Caninae*, and to what extent.

Progeny homogeneity

Morphological studies on wild material of Nordic dogroses, grown in a randomized design in an experimental field, have recently been carried out at Balsgård in South Sweden (Nybom et al. 1996, 1997). Species discrimination could be achieved with morphological markers when a multivariate approach was applied. In addition, considerable differences were found between the species in the amount and distribution of intraspecific genetic variation. *Rosa rubiginosa* appears to be the most homogeneous of the investigated species, whereas *R. dumalis* is the most heterogeneous. Recently, RAPD markers applied to the same material have given similar results (Å. Olsson, manuscript in preparation).

In keeping with *R. rubiginosa* being more homogeneous than *R. dumalis*, our *R. rubiginosa* × *R. dumalis*

offspring are more homogeneous than the offspring in the reciprocal cross, in all the characters investigated. Moreover, the cross *R. rubiginosa* × *R. dumalis* showed fewer pollen donor bands than offspring of the reciprocal cross. Gustafsson (1944) made a pair of reciprocal crosses with *R. rubiginosa* and *R. canina*, and reports progenies with *R. rubiginosa* as seed parent to be more homogeneous than those of the reciprocal cross, although he only had six plants from the latter cross. In conclusion, a close relationship may be inferred between, on the one hand, degree of species homogeneity and, on the other hand, meiotic marker distribution. Further analyses of marker distribution should become an important tool in the research of dogrose evolution and systematics.

RAPD marker segregation

Abberrant Mendelian segregation ratios may be brought about by linkage between nuclear genes and distorting factors such as disturbances in both the pre- and postzygotic phases of reproduction (Zamir and Tadmor 1986). The disturbance seems to be higher in interspecific crosses since many of the loci regulating the phases of reproduction then are heterozygous, thereby leading to unbalanced reproduction. Segregation distortion has, nevertheless, also been reported in intraspecific crosses in several plant species (Gomez et al. 1996; Jenczewski et al. 1997).

Some segregation data were reported by Debener et al. (1997) from an interspecific cross between *R. obtusifolia* Desv. and *R. sherardii*, both in sect. *Caninae*. Five plants were obtained, all of which morphologically resembled the seed parent more than the pollen parent. According to RAPD data, however, each offspring plant inherited 58–67% of the 24 pollen parent-specific markers. Moreover, of these 24 pollen donor markers, 90% were transmitted to at least one of the progeny plants. Debener et al. (1997) made no reference to the *Caninae* meiosis, and did apparently not investigate the inheritance of seed parent-specific markers.

The segregation distortion found in our RAPD data is much greater than any that has been previously reported, and it is most likely to be a reflection of the *Canina* meiosis. The influence from the seed parent was very pronounced since all but one of the seed parent markers were inherited by all plants in each cross. By contrast, only half of the pollen donor markers were found in any of the offspring. Of the 10 pollen markers transmitted, 6 appeared in approximately 80% of the plants, one in 50% and three in 10%. These data do not fit a model in which the same two genomes are involved in all bivalent formation, as would be expected in allopolyploid dogroses with two homologous genomes (Grant 1971).

Acknowledgements Valuable comments on the manuscript were given by Prof. H. C. Prentice. Financial support was given by the Swedish Research Council for Forestry and Agriculture. The experiments performed comply with current Swedish laws.

References

Almquist S (1919) Sveriges rosor. Idun, Stockholm

Ben-Meir H, Vainstein A (1994) Assessment of genetic relatedness in roses by DNA fingerprinting analysis. Sci Hortic 58: 115–121

Blackburn K, Heslop-Harrison JW (1921) The status of the British rose forms as determined by their cytological behaviour. Ann Bot 35: 159–188

Cole P, Melton B (1986) Self- and cross-compatibility relationships among genotypes and between ploidy levels of the rose. J Am Soc Hortic Sci 111: 122–125

Debener T, Bartels C, Mattiesch L (1996) RAPD analysis of genetic variation between a group of rose cultivars and selected wild rose species. Mol Breed 2: 321–327

Debener T, Bartels C, Spehtmann W (1997) Parentage analysis in interspecific crosses between rose species with RAPD markers. Gartenbauwissenschaft 62: 180–184

Fagerlind F (1940) Sind die *canina*-Rosen agamospermische Bastarde? Svensk Bot Tidskr 34: 334–354

Gallego FJ, Martinez I (1996) Molecular typing of rose cultivars using RAPDs. J Hortic Sci 71: 901–908

Graham GG, Primavesi AL (1993) Roses of Great Britain and Ireland. BSBI handbook no. 7. Botanical Society of the British Isles, London

Grant V (1971) Plant speciation. Columbia University Press, London New York

Gomez R, Angel F, Bonierbale M, Rodriguez F, Tohme J, Roca WM (1996) Inheritance of random amplified polymorphic DNA markers in cassava (*Manihot esculenta* Crantz). Genome 39: 1039–1043

Gustafsson Å (1944) The constitution of the *Rosa canina* complex. Hereditas 30: 405–428

Gustafsson Å, Håkansson A (1942) Meiosis in some Rosa-hybrids. Bot Not 23: 331–343

Holm S (1995) Unexpectedly high levels of genetic variation in *Potentilla argentea* L. (s.l.) in southern Sweden. Hereditas 123: 127–139

Hubbard M, Kelly J, Rajapakse S, Abbott A, Ballard R (1992) Restriction fragment length polymorphisms in *Rosa* and their use for cultivar identification. HortScience 27: 172–173

Jenczewski E, Gherardi M, Bonnin I, Prosperi JM, Olivieri I, Huguet T (1997) Insight on segregation distortions in two intraspecific crosses between annual species of *Medicago* (Leguminosae). Theor Appl Genet 94: 682–691

Jicinska D (1976a) Autogamy in various species of the genus *Rosa*. Preslia 48: 225–229

Jicinska D (1976b) Morphological features of F_1 generation in *Rosa* hybrids. 1. Hybrids of some species of the sect. *Caninae* with *Rosa rugosa*. Folia Geobot Phytotax 11: 301–311

Kroon GH, Zeilinga AE (1974) Apomixis and heterogamy in rose rootstocks (*Rosa canina* L.). Euphytica 23: 345–352

Melville R (1960) A metrical study of leaf-shape in hybrids. I. The leaf-shape of some F_1 hybrids and their parents. Kew Bull 14: 88–102

Melville R (1975) *Rosa* L. In: Stace CA (ed) Hybridization and the flora of the British Isles. Academic Press, London, pp 212–227

Millan T, Osuna F, Cobos S, Torres AM, Cubero JI (1996) Using RAPDs to study phylogenetic relationships in *Rosa*. Theor Appl Genet 92: 273–277

Norusis MJ (1990a) SPSS® Base systems user's guide. SPSS, Chicago

Norusis MJ (1990b) SPSS® Advanced statistics™ user's guide. SPSS, Chicago

Norrmann GA, Quarin CL (1987) Permanent odd polyploidy in a grass (*Andropogon ternatus*). Genome 29 : 340–344
Nybom H, Olsson A, Werlemark G (1996) Morphometric variation in Nordic dogroses (*Rosa* sect. *Caninae*, Rosaceae). Acta Univ Ups Symb Bot Ups 31 : 59–68
Nybom H, Carlson-Nilsson U, Werlemark G, Uggla M (1997) Different levels of morphometric variation in three heterogamous dogrose species (*Rosa* sect. *Caninae*, Rosaceae). Plant Syst Evol 204 : 207–224
Rieseberg LH, Ellstrand NC (1993) What can molecular and morphological markers tell us about plant hybridization? Crit Rev Plant Sci 12 : 213–241
Roach DA, Wulff RD (1987) Maternal effects in plants. Annu Rev Ecol Syst 18 : 209–235
Rowley GD (1967) Chromosome studies and evolution in *Rosa*. Bull Jard Bot Natl Belge 37 : 45–52
Smith-White S (1955) The life history and genetic system of *Leucopogon juniperus*. Heredity 9 : 79–91
Täckholm G (1920) On the cytology of the genus *Rosa*. Svensk Bot Tidskr 14 : 300–311
Torres AM, Millan T, Cubero JI (1993) Identifying rose cultivars using random amplified polymorphic DNA markers. HortScience 28 : 333–334
Vainstein A, Ben-Meir H (1994) DNA fingerprint analysis of roses. J Amer Soc Hort Sci 119 : 1099–1103
Wissemann V, Hellwig FH (1997) Reproduction and hybridisation in the genus *Rosa* Section *Caninae* (Ser.) Rehd. Bot Acta 110 : 251–256
Zamir D, Tadmor Y (1986) Unequal segregation of nuclear genes in plants. Bot Gaz 147 : 355–358
Zielinski J (1985) Studia nad radzajem *Rosa* L. Systematyka sekcji *Caninae* DC. em. Christ. Arbor Körnickie 30 : 3–109