Translocation Heterozygosity in *Phlox drummondii*

K. J. Madhusoodanan,¹ M. A. Nazeer² and G. V. Subrahmanyam

National Botanical Research Institute, Lucknow, India

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Swapping of two fragments, due to breaks in non-homologous chromosomes, results in an interchange complex involving four chromosomes of the complement, which, despite its accompanying sterility, has selective advantage for the outbreeders that have undergone enforced inbreeding. The reason being that it facilitates the conservation of allelic heterozygosity and, therefore, promoting immediate fitness at the expense of flexibility (see Stebbins 1950, John 1976). When such heterozygotes arise they "float" in a population and if they have any adaptive value, they get selected, spread and finally fixed in the populations. The interchange heterozygote found in *P. drummondii*, a garden annual, represents a case of "floating" heterozygosity. The species has been regarded to be basically self-incompatible and obviously is an obligate outbreeder (cf. Erbe and Turner 1962, Levin 1978). However, the present investigation throws light on some changes which have occurred in breeding and meiotic systems under the garden conditions in an ecogeographically different region from its native habitat.

Material and methods

The material on which the study is based is *Phlox drummondii* Hook. grown in the garden of NBRI. Its flowers are red (Tyrian rose 24 in Hort. colour chart) with non-frilled corolla.

Young flower buds were fixed in Carnoy's fluid to which little ferric acetate was added. Squashes of anthers were prepared in iron-acetocarmine following the usual technique. Leaf tips were fixed in acetic alcohol (1:3) after PDB pre-treatment for two hours and stained in Feulgen. Estimate of pollen fertility was based on its stainability in 1% acetocarmine.

Observations

Meiosis

P. drummondii is diploid with 7 bivalents at metaphase I (Fig. 1). On an average 4.63 are ring and 2.37 are rod bivalents. The number of chiasmata per cell ranges from 11 to 16, while the mean number is 13.15 out of which only 8.58 are terminalized giving a terminalization coefficient of 0.65. The subsequent course of meiosis is normal, resulting in 96.4% stainable pollen and good seed setting (Table 1).

The translocation heterozygote revealed at diakinesis and metaphase I a com-

¹ Present address: Indian Cardamom Research Institute, Kailasanadu - 685 553, Kerala, India.

² Present address: Rubber Research Insutitute of India, Kottayam Pin-686 009, Kerala, India.

plex of 4 chromosomes plus five bivalents (Figs. 2-3). The nucleolar chromosomes were not involved in the association. However, in the majority of cells (70%) the

Table 1. Chromosome association at metaphase I and pollen fertility

Taxon	No. of cells analysed	Associations (%)		Types of complexes (%)		Mean chiasmata per cell	Termination coefficient	Pollen fertility (%)
		7 II	1 IV+5 II	Ring	Chain			
Homozygote	80	100	—	—	—	13.15	0.65	96.40
Heterozygote	80	70	30	75	25	13.75	0.54	90.92

Figs. 1-7. 1, metaphase I, 7 II (homozygote). 2-7. Interchange heterozygote. 2-4, metaphase I, R_{IV}+5 II; R_{IV}+5 II and 7 II respectively. Note adjacent orientation and interstitial chiasmata of the ring. 5-6, anaphase I. Note late disjunction of 2 bivalents in the latter. 7, photo-idiogram of the karyotype of normal (a) and interchange heterozygote (b). Heteromorphic pairs are marked. Figs. 1-6. $\times 1500$. Fig. 7. $\times 2000$.

two pairs involved in the interchange failed to synapse resulting in two bivalents (Fig. 4). Seventy five per cent of the cells with the complex exhibited rings while the rest had chains (Table 1). No unpaired chromosome or numerically uneven multiples were observed. In the interchange multiples, chiasmata are mostly localised in the terminal portion, but 7.5% of the cells have interstitial chiasmata (Fig. 3). Chiasma frequency per cell ranges from 11 to 18. On an average 13.75 chiasmata are formed, out of which 7.48 are terminal giving a terminalization coefficient of 0.54.

The orientation of the multiples at metaphase I is predominantly disjunctional. While almost all of the chain configurations show an alternate disjunctional orientation, in few of the rings, adjacent chromosomes are directed to the same pole (Fig. 2). However, in more than 75% cases there is alternate disjunction. While the cells with interchange multiple segregated normally at anaphase I (Fig. 5), those cells in which the interchange multiple was in the form of 2 bivalents, there was delay in disjunction of the 2 members of the bivalents (Fig. 6). The pollen stainability was near normal (90.92%), as also was the seed setting.

Karyotype

The normal *P. drummondii* cultivar has 14 chromosomes in 7 homomorphic pairs (Fig. 7a) with a basikaryotype formula of 5L+2J. The satellite pair is submedian (L) and is fifth in the order of length. The subterminals (J) are the smallest. A karyotypic study of the translocation heterozygote reveals heteromorphism in the second and last pair of the complement (Fig. 7b).

Discussion

The species of *Phlox* are preponderantly diploid with a base number of seven. So the homozygous forms of *P. drummondii* regularly form 7 bivalents at meiosis while the heterozygote reveals multiple association of four chromosome as a ring or a chain in 30% of the total cells examined. Notwithstanding the fact that in majority of the cells only bivalents were discernible, the present case is a clear instance of interchange translocation. Cases are on record in which an occasional chain configuration is the only evidence of the presence of a translocation (e.g. maize: Clark and Anderson 1935, barley: Burnham *et al.* 1954).

A comparison of metaphase I pairing of homo- and heterozygote reveals that the terminalization coefficient is lower in the latter (0.54) than in the other (0.65). Obviously it is due to the heterozygous nature of chromosome arms which impedes terminalization of chiasmata in the heterozygote. Since, in the heterozygote, ring configuration was frequent it can be assumed that the size of the exchanged segments is not small (cf. Burnham 1954). The asymmetrical nature of the interchange involving the long arm of the two non-homologous chromosomes of the second and last pair is apparent from the presence of two heteromorphic pairs in the karyotype.

It has been pointed out that homobrachial chromosomes as well as the terminal chiasmata facilitate regular disjunction of interchange complex (Darlington

1937). But in the present case chromosomes involved in translocation are sub-metacentric or subtelocentric and the chiasmata are also not always terminal. So it follows that the prevalent alternate orientation may be due to some phenomenon like the 'pre-metaphase stretch' as suggested by John and Lewis (1957) in *Periplaneta americana*.

The fertility of an interchange heterozygote depends largely upon the frequency of multiple complex(es) and its orientation. As observed in *Gaillardia pulchella* (Stontamire 1955), *Zea mays* (Thomas 1961), *Bougainvillea* (Zadoo and Khoshoo 1968) and also in the induced interchange heterozygotes of *P. drummondii* (Dhillon and Dhillon 1974) the present interchange hybrid is highly fertile (ca. 90%). In this connection, it is worth recalling that Stebbins (1950) postulated that the chromosomal abnormality at meiosis leading to the production of a certain percentage of inviable gametes is relatively small when single translocation is involved. Good seed setting on selfing in the *Phlox* heterozygote confirms the viability of pollen grains. Probably, it suggests that the deficiencies and duplications caused by translocation do not have serious physiological imbalance on the gametes and that its genome can withstand minor rearrangements. Presumably, the high fertility in the present material can be correlated with predominate alternate disjunction of the chromosomes at anaphase I and low frequency (7.5%) as well as reciprocal nature of interstitial chiasmata (see Burnham 1956).

Uniformity is favoured under the garden conditions which is usually attained by inbreeding and selection resulting in a progressively limited size of breeding group. In such instances the heterozygous gene sequence maintained by interchange is at an advantage due to isolation associated with migration and also by cultivation in diverse habitats. Superimposed on this, adaptive advantage by way of heterosis is also conferred in a number of diploid ornamentals like *Canna*, *Amaryllis*, *Bougainvillea*, *Crinum*, *Gloriosa*, *Hemerocallis* and *Plumeria* (Khoshoo 1968) which too holds true for the present case.

The low frequency of interchange heterozygosity i.e. five per cent, in the present case points towards its "floating" nature. However, due to enforced inbreeding under garden condition the interchange heterozygote may confer some adaptive value and become fixed and spread in the species. The high fertility value of the present interchange can also be inferred from the high frequency of normal disjunction achieved after interchange event.

Summary

In an individual belonging to one of the diploid garden races of *Phlox drummondii* Hook. ($2n=14$), in 30% of the cells, four chromosomes instead of forming two bivalents at meiosis form an interchange association. Except for its heterotic behaviour, the translocation heterozygote was phenotypically indistinguishable from the homozygote. The chromosome complex was both of ring and chain type, the former being preponderant. At anaphase I, in the exclusively bivalent forming cells, disjunction of two of the bivalents was consistently late. The asymmetrical nature of the interchange as well as the involvement of the long arm of two non-

homologous chromosomes of second and last pair of the complement is apparent from the two heteromorphic pairs in the karyotype. Pollen fertility and seed setting were near normal. The establishment of interchange heterozygosity is correlated with a change of breeding system from out-to inbreeding.

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