Viscum album in Japan: Chromosomal Translocations, Maintenance of Heterozygosity and the Evolution of Dioecy

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The genus Viscum is very suitable for study of structural rearrangements in chromosomes, having very large chromosomes, low basic number and very little polyploidy. An extensive survey of the dioecious species V. album (n=10) in Japan has revealed the widespread occurrence of several different chromosomal translocation complexes. Male plants are always heterozygous for large sex-associated translocation complexes, having 6II O8 (six bivalents and a ring-of-eight) or 5II O10 or rarely 4II O12 at meiosis. Female plants are homozygous for these complexes, usually having 10II. There is also a floating O4 which occurs in both male and female plants. Female plants may be heterozygous for another O4 or O6, which do not occur in male plants. Models are presented to account for the relationship between all of the translocations involved.

The high levels of translocation heterozygosity are probably important in maintaining heterozygosity in the species for large complexes of adaptive genes. However the sex-associated permanent translocation heterozygosity may have originally been established as a mechanism to stabilize dioecy based on non-allelic, unlinked genes for maleness and femaleness.

Key words: Chromosomal translocations — Dioecy — Sex-associated translocations — Viscum album

Chromosomal rearrangements through reciprocal translocations are well known in plants. They involve the exchange of chromosome segments between different chromosomes, thus producing new sequences of chromosome ends. An individual heterozygous for a reciprocal translocation will therefore produce a multivalent ring of chromosomes at meiosis. If adjacent chromosomes move together at anaphase, duplication and deletion of whole chromosome arms will result and the resulting cells will be inviable. Genetically balanced products of meiosis will normally be produced only when the chromosomes in the ring segregate alternately to different poles, and alternate segregation occurs regularly in plant species in which translocations have been established in the genetic system. This can be recognized at meiotic metaphase by the characteristic “zig-zag” orientation of the ring (Fig 1). As a result, the translocated chromosomes are inherited together, so that they behave genetically like a single linkage group. Translocations therefore conserve large linkage groups in which adaptive gene complexes can accumulate by natural selection.
Fig. 1. Multivalent rings in *Viscum* showing alternate (zig-zag) arrangement of chromosomes.

a: Q4 resulting from one translocation. b: Q6 resulting from two translocations involving three pairs of chromosomes.

The occurrence of heterozygosity for chromosomal translocations in plant populations is usually explained as an adaptive response to high levels of inbreeding. In the classical cases of *Oenothera*, *Rhoeo* and *Isotoma*, translocation heterozygosity in inbreeding populations is maintained in all individuals by systems of balanced lethal genes which eliminate the homozygotes (James, 1970; Cleland, 1972). In other cases, for example in *Clarkia* (Bloom, 1977), high levels of translocation heterozygosity appear to be maintained in natural populations by selection generated when high levels of inbreeding are enforced by environmental conditions. Chromosomal translocations are clearly an important mechanism utilized in natural populations for the maintenance of genetic heterozygosity for large adaptive gene complexes.

In some dioecious plant species, permanent translocation heterozygosity has been achieved, at least in one sex, through the association of the translocations with the sex determination system. A translocation multivalent is thus characteristic of the heterozygous sex. Sex multivalents are well known in male plants of *Humulus* (Ono, 1937) and *Rumex* (Smith, 1972). In animals, multiple sex chromosome systems generating multivalents are well known in many phyla, and have often arisen through translocations between autosomes and the sex chromosomes. White (1973) has argued that the adaptive value of such systems is again the fixation of a great deal of genetic heterozygosity, even though it occurs in one sex only.

Studies in the mistletoe genus *Viscum* have revealed permanent sex-associated translocation heterozygosity in the majority of the dioecious species, distributed through Africa, Europe and Asia (Wiens and Barlow, 1973, 1975, 1979; Barlow and Wiens, 1975, 1976; Barlow et al. 1978; Mechelke, 1976). In these species, male plants consistently show a multivalent at meiosis, ranging from a ring-of-four (Q4) to Q6, Q8, Q10 and even Q12. In addition, there are high levels of floating translocation heterozygosity, that is, of translocations which are not sex-associated, and not maintained by balanced lethals, so that both homozygotes and heterozygotes may occur in either sex. In a number of cases the frequencies of heterozygosity are so high that their maintenance by positive selection for the translocation heterozygotes seems likely.