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Unravelling Chromosomal Behaviour in *Clematis grata*: The Role of Cytomixis in Pollen Formation

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Clematis grata Wall., a climbing plant of the family Ranunculaceae, occurring in the Himalaya, shows great variation in chromosome behaviour during pollen formation. Meiotic studies of Himachal Pradesh, Kashmir and Uttarakhand revealed an interesting phenomenon known as cytomixis, in which chromatin moves from one pollen mother cell (PMC) to another. Such a strange chromosome transfer was noticed during early prophase I to the tetrad stage and sometimes in clusters of adjacent PMCs. This event resulted in a number of differently sized chromosome complements being found in the resulting PMCs. Other irregularities in meiosis, such as unoriented bivalents and lagging chromosomes, were also observed, as were chromatin bridges and extensive stickiness of the chromosomes. Such abnormalities interfered with normal microsporogenesis and caused the production of micronuclei and pollen of unequal size, which led to low pollen fertility. Since the cytomixis phenomenon was found in several populations, it is probable that it has a genetic basis and may play a role in chromosome variation and reproductive diversity in natural populations of *C. grata*. The findings reveal the possibility that small differences in meiosis may affect the state of pollen development, their fertility and consequently, the adaptability of plant species in the Himalayas.

A microscopic journey into chromosome behaviour, pollen fertility and plant diversity

The Western Himalayas are a treasure house of plant diversity. The region is characterised by an amazing diversity of flowering plants living in a variety of climatic and ecological conditions, from foothills to the high-altitude mountains. One of these plants is *Clematis grata* Wall., a perennial climbing shrub of the family Ranunculaceae. While this plant looks like a normal climber in the Himalayan vegetation, a study of its reproductive cells shows an amazing tale of meiotic abnormalities and pollen formation. The cytological studies of *Clematis grata* have given us a surprising finding, namely a phenomenon called cytomixis, which occurs when genetic material is transported from one pollen mother cell to another. This phenomenon can disturb normal meiosis and ultimately influence pollen fertility and reproductive success. *Clematis grata* is a perennial climber, typically growing in tropical, subtropical and temperate areas. In the Himalayas, it has been recorded at altitudes ranging from 800 m to 3,000 m. Stems are deeply furrowed, with pinnately compound leaves, and attractive cup-shaped white flowers with hairy peduncles. It is also known as an ethnomedicine species. Traditional applications of *C. grata* are reported for other Himalayan neighbouring regions, including its use in folk medicine for jaundice and external burns. However, it was not the medicinal potential of this species that piqued our interest, but rather its chromosomes.

Cytomixis is one of the most interesting phenomena noted in *Clematis grata*. Transfer or migration of chromatin, the material containing chromosomes, from one cell to another by way of connections or channels in the cytoplasm is called cytomixis. Basically, neighbouring pollen mother cells can get linked together, so that chromatin can pass between them. In *C. grata*, cytomictic connections were observed between two or several neighbouring PMCs. Chromatin transfer was observed at early meiotic stages and until the tetrad. Some of the PMCs received extra chromatin and were termed hyperploid; others lost chromatin and were termed hypoploid. The transfer of chromatin to a neighbouring cell was also seen to be extensive in some cases, leaving the original cell with an apparently empty PMC. There were other irregularities observed besides cytomixis. The abnormal chromatin movement was accompanied by several other abnormalities.

1. **Chromosomal stickiness**: Occasionally chromosomes were found to stick together and behave as an aggregate instead of individual entities. Some populations showed a high incidence of chromosomal stickiness.
2. **Unoriented bivalents**: Metaphase- I was characterised by the presence of some chromosome pairs that did not orient on the equatorial plate normally. Abnormal orientation can disrupt the following separation of chromosomes.
3. **Laggard chromosomes**: In anaphase and telophase, some chromosomes did not reach the correct poles and were left behind. These are referred to as laggards.
4. **Chromatin bridges:** Other peculiarities observed were chromosomal bridges during anaphase and telophase. The chromosome material did not divide neatly into two daughter populations but seemed to be linked between the two.
5. **Micronuclei:** Small extra nuclei called micronuclei may develop from fragments of chromosomes or surplus chromatin materials which are not attached to the bulk of the daughter nuclei. All of these abnormalities can eventually lead to abnormal development of normal microspores and pollen grains.

The effects of cytomixis on abnormal meiosis to abnormal pollen

The effects of cytomixis are more pronounced at the later stages of pollen development. In *C. grata,* abnormal microsporogenesis produced monads, dyads, triads and polyads, which were sometimes accompanied by micronuclei, rather than the usual four microspores. The pollen grains produced were also variable in size. Occurrence of fertile and sterile pollen grains was observed, which indicated a disturbed meiotic process. Cytomixis is at first sight a harmful event as it can affect meiosis and pollen fertility. But biological significance may be more complicated. Pollen mother cells of cytomixis may have varying chromosome complements. Chromosomal variation can sometimes result in the occurrence of abnormal gametes and, over time, may affect genetic and cytological diversity. For this reason, cytomixis has been much noticed by plant cytologists. It has been reported in many flowering plants and can develop by several mechanisms, such as genetic factors, physiological conditions and environmental stresses. Cytomixis has been observed more than once in geographically distant samples of *Clematis grata,* and we proposed that this phenomenon might have a significant genetic basis and not represent a preparation artefact of the slides (Rani et al 2010; Rani et al 2013: Singhal et al 2016). On first glance, the cytology of a wild Himalayan climber might seem a long way from agriculture. But knowledge of the behaviour of chromosomes is vital to plant breeding, genetic conservation and crop improvement. Meiosis is the link between generations.

Mutations affecting meiosis may affect:

- Pollen viability;
- Seed production;
- Genetic variability;
- Chromosome number variation;
- Changes in populations of plants over time.

The study of wild plants like *Clematis grata* thus offers useful insights into the spontaneous processes of plant genetic variation and maintenance. The Western Himalayas with its very large environmental gradients on short geographical distances offer an ideal natural laboratory for the study of such phenomena.

Conclusion

Even the beautiful Himalayan climber *Clematis grata* Wall. has a hidden world of chromosomes. It has a stable basic chromosome number 2n = 16, but its pollen mother cells show very irregular meiosis. As a result of cytomixis from early meiotic stages up to tetrads, chromatin can be redistributed between neighbouring PMCs and hypo- and hyperploidy are produced. Together with chromosomal stickiness, laggards, bridges and micronuclei, this causing abnormality in microsporogenesis and low pollen fertility. Cytomixis is, therefore, not just a microcursory spot of interest but a key to understanding the mechanisms of chromosomal variation and how they relate to plant fertility and evolution.

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