On the chromosome pairing in six hybrids among four Geum species

by

W. GAJEWSKI

Botanic Garden of the University of Warsaw.

I have found in six interspecific hybrids among *Geum rivale* L., *G. urbanum* L., *G. aleppicum* Jacq. and *G. macrophyllum* Willd. rather peculiar relationships in the chromosomal conjugation at meiosis. In P. M. C's either a type of meiosis occurs with most of the cells with normal pairing and only few (2—6) univalents, or, in other hybrids, in all cells only few bivalents were to be found, most of the chromosomes remaining unpaired. No intermediate degree of chromosome pairing was found in any of the studied hybrids.

All four species and their hybrids have the same somatic chromosome numbers 42 and could be regarded as hexaploid. They have very similar karyotypes. In all six hybrids described here I have found no differences between reciprocal crosses as regards their morphology, fertility or degree of chromosome pairing. So, the influence of the cytoplasm on the phenomena described here seems to be excluded.

The degree of chromosome pairing of the hybrids among four species mentioned above was as follows:

No.	Hybrid	Numbers of P. M. C' s with no. of univ.:															
		0	2	4	6	8	....	28	30	32	34	36	38	40	42	n	M
1	*G. urbanum x rivale*	38	8	4	1	—	—	—	—	—	—	—	—	—	—	51	1,5
2	*G. aleppicum x rivale*	40	14	6	—	1	—	—	—	—	—	—	—	—	—	61	1,6
3	*G. aleppicum x macrophyllum*	21	9	4	1	—	—	—	—	—	—	—	—	—	—	35	1,7
4	*G. macrophylum x rivale*	—	—	—	—	—	—	1	5	2	6	5	4	5	3	31	35,6
5	*G. aleppicum x urbanum* *)	—	—	—	—	—	—	—	2	6	5	6	8	1	2	30	35,5
6	*G. urbanum x macrophyllum*	—	—	—	—	—	—	—	6	3	5	8	8	2	—	32	34,9

*) The degrees of chromosome pairing of some hybrids described here, given in Proceedings of the Eighth Intern. Congress of Genetics (p. 578) were not exact due to unsuitable aceto-carmine method used before.

The course of meiosis in hybrids Nos. 1—3 is very similar and quite regular. The rare univalents in most cases segregate undivided at I—A. and after the second division the tetrads look quite normally. The degeneration of the young pollen grains usually takes place before or at the first pollen mitosis.

The meiosis in hybrids Nos. 4—6 has nearly the same very irregular course. The few bivalents are to be found in I—M. at the equatorial plane and the numerous univalents are scattered on the whole spindle showing a pronounced tendency to be grouped around both poles. After the bivalents separation they are segregated at random to both daughter nuclei. Many restitution nuclei arise as the result of univalents movement delay. The second division is also highly irregular leading to very abnormal tetrads. A more detailed description of the univalents behaviour in different types of meiosis in *Geum* hybrids was given previously (G a j e w s k i, 1949). The reader interested in the cytological peculiarities of *Geum* hybrids is refered to this paper.

The six hybrids mentioned above differ not only in their type of chromosome pairing but also in their vigour and fertility. Of course, they differ in their morphology too, beeing in most traits intermediate between their respective parents. The morphological analysis of parental species and hybrids will be published in a special paper. The vigour and fertility of the studied hybrids were as follows:

No.	Hybrid	Vigour	Good pollen	Good seeds
1	*G. urbanum x rivale*	equal to parental species	85—90%	80—100%
2	*G. aleppicum x rivale*	equal to parental species	16—20%	10— 15%
3	*G. aleppicum x macrophyllum*	sublethal, deformed flws.	0%	0%
4	*G. macrophyllum x rivale*	distinct hybrid vigour	0,7%	0,5%
5	*G. aleppicum x urbanum* *)	distinct hybrid vigour	0,5%	0,06%
6	*G. urbanum x macrophyllum*	sublethal, deformed flws.	0.1%	0%

As we can easily see from the two tables there is any correlation among the degree of fertility, the vigour of the hybrids and the degree of chromosome conjugation. We can only state that all the hybrids with high degree of asynapsis are also sterile which is obviously the result of the great disturbances in their meiotical

divisions. The hybrids 3 and 6 with many disturbances in their growth, which are also manifested in numerous malformations in floral organs are both sterile notwithstanding the fact that one of them has nearly normal meiosis. In hybrids Nos. 1 and 2 which both are vigorous and with the same high degree of chromosome pairing the differences in their fertility are very striking showing that fertility is not directly correlated with the degree of chromosome pairing.

A very interesting fact is also the lack of correlation between the degree of chromosome conjugation and fertility of the hybrids from one side and the morphological differentiation and taxonomical position of the crossed species from the other side. All four species studied here belong to the subgenus *Eugeum* F o c k e which is caracterised by the geniculate structure of the styles. The styles are divided by a loop in two parts: the lower so called rostrum persisting on the fruits and forming hook-like structure, and the upper stigmatal part which falls down after the fertilization. In this subgenus two sections were distinguished: one sect. *Gmeliniana* T r a t t i n., to which belongs *G. rivale,* comprises species with paucifloral shoots, with large flowers and with long, slender stigmatal part of the styles which is usually longer than the half of the rostrum. The second section *Murrayana* T r a t t i n., to which belong all other three species studied here, comprises species with multifloral shoots, with small or medium flowers and with a short stigmatal part (from 1/3 to 1/4 of rostrum length).

The most fertile hybrid *G. rivale* x *urbanum* is just between two species which belong to two different sections. *Geum rivale* differs from *Geum urbanum* in nearly every trait and especially in shape, size and colour of petals, in the development of the gynophore, in the position of petals and sepals, in the structure of styles and so on. In all these traits the three other species from the section *Murrayana* are much more alike, but the hybrids among them are sterile and two of them show a high degree of asynapsis.

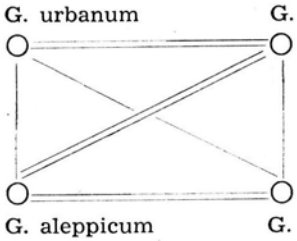
From the geographical point of view the four species studied here possess the largest areas in the whole genus. The area of *G. rivale* covers the greater part of the Holarctis: North and Central Europe to East Sibiria in Asia and a great part of Atlantic and Central North America. The area of *G. aleppicum* is extended from Poland on the west through the whole Eurasiatic continent eastward and over the whole North American continent to Mexico on the south. The area of *G. urbanum* is of the European type covering whole

Europe except the most northern parts and eastward extending to West Sibiria and Central Asia. *Geum macrophyllum* is an American species with a wide area in North America. From the geographical point of view *Geum urbanum* as an European species and *G. macrophyllum* as an American one are the most separated species, wheras *G. rivale* and *G. aleppicum* occupy more intermediate positions.

Discussion.

Now a question arises how to interprete the relationships described above. I would like to suggest one possible interpretation. Some preliminary premises must be done. It is highly probable that all four *Geum* species studied here are monophyletic having some common ancestors in the more or less far past. They have diverged and formed separate species by a process of gradual accumulation of many genic differences through the period of their evolution. The results of genic analyses of the hybrid *urbanum* x *rivale* done by Marsden-Jones(1930), Prywer (1932) and the author and on the hybrid *G. aleppicum* x *G. rivale* (unpublished data of the author) show that these species differ in many genes. Some specific traits are segregating in simple ratios indicating differences in few genes but most other give a „continuous" segregation indicating differences of polygenic nature. For the other species such direct evidence is lacking as the hybrids among them are sterile. The nearly complete chromosomal conjugation in the hybrids *G. urbanum* x *rivale*, *G. aleppicum* x *rivale* and *G. aleppicum* x *macrophyllum* shows that all four species have similar chromosomal structure with not very pronounced structural differences in their chromosomal sets. The lack of any intermediate degree of pairing among the six hybrids studied here indicates that probably some few or single steps like mutations in certain points result in change from nearly normal pairing to very pronounced asynapsis in the hybrids. It seems that asynapsis, lack of vigour in some hybrids and degree of fertiliy of different hybrids are quite unrelated phenomena caused probably by different factors acting specifically on the degree of pairing (reducing chiasmata formation or causing premature desynapsis), on the degree of gametic viability or on the viability, growth and differentiation of hybrid zygotes. All these factors cause effective physiological barriers among species and have probably played a major role in the process of their differentiation.

The results obtained here could be represented schematically like this:



The double lines indicating high degree of chromosome pairing in the hybrids and the single ones lack of pairing (asynaptic hybrids). These results could be tentatively interpreted as follows: *Geum rivale* and *G. aleppicum* represent some kind of intermediate link between *Geum urbanum* from one side and *G. macrophyllum* from the other. The above diagram could also be represented in the following manner:

1. G. urbanum,←2. G. rivale,↔3. G. aleppicum,→4. macrophyllum.

This scheme indicating that for the relationship of *G. aleppicum* to *G. rivale* nothing decisive could be said but that *G. urbanum* is more related to *G. rivale* as to any other species and *G. macrophyllum* to *G. aleppicum* in the same way as *G. urbanum*. This scheme indicating only the relationships in chromosome pairing does not fit to the relations in viability and fertility of the respective hybrids. It is now impossible to say if this scheme depicts the ways of specific differentiations in the evolution of the hexaploid *Geum* species. The lack of any correlation between the taxonomic position of the crossed species and the degree of chromosome pairing in respective hybrids seems to give a rather negative evidence for such assumption. From the other side the geographical evidence from the distributional areas of these species is consistent with our scheme as *G. urbanum* and *G. macrophyllum* are the most separated species, beeing European, and American respectively, while *G. rivale* and *G. aleppicum* having large areas both in Eurasia and America occupy more intermediate positions.

LITERATURE CITED.

Gajewski, W. 1949. On the univalents behaviour at meiosis in some interspecific *Geum* hybrids.-Hereditas 35, 221—241.

Marsden-Jones, E. M. 1930. The genetics of *Geum intermedium Willd. Ehrh.* and its back-crosses. J. of Genet. *23*, 377—395.

Prywer, C. 1932. Genetische Studien über die Bastarde zwischen *Geum urbanum* L. and *G. rivale* L. — Acta Soc. Bot. Pol. *9*, 87—144.