# Evolutionary Significance of Chromosome Size and Chromosome Number in Plants

By Dontcho Kostoff

*(Institute of Genetics, Academy of Sciences of U.S.S.R., Moscow)*

POLYPLOIDY in plants is a very common phenomenon. Its evolutionary significance was first recognized by Winge[1] (1917) about twenty years ago and is generally accepted at the present time.

The behaviour of the chromosomes of various sizes in diploid and polyploid plants, which I have studied recently,[2] and those studied by other investigators, suggested that the size of chromosomes may play an important rôle in the survival of the polyploids, *e.g.*, in the evolution of plants. The studies on the chiasma frequency in long and short chromosomes[3–8] and even in long and short arms of one and the same chromosome[9] showed that the mean number of chiasmata per bivalent and per arm is approximately proportional to the length of the pairing blocks. This ratio breaks down for very small chromosomes,[10–12] *i.e.*, when there is a wide range in chromosome length, but even in these cases long chromosomes have more chiasmata per bivalent than the short ones.

Studying cytologically a series of autopolyploid plants with various chromosome lengths, the following tendencies [4,13–15] have been found: (1) longer chromosomes form more frequently quadrivalent groups during the meiosis than the shorter ones. The very short ones usually do not form quadrivalent groups. (2) Autotetraploid plants, derived from species with long chromosomes, form quadrivalents more frequently (when the chromosome number is not too large) than tetraploids derived from species with short chromosomes; in other words the coefficient of quadrivalency

$$\left(\frac{\text{Number of the quadrivalents formed}}{\text{Number of the quadrivalents that can be formed}}\right)$$

is much greater in the former autotetraploids than in the latter. (It may vary from 1 to 0.) These tendencies are best interpreted on the pairing blocks hypothesis (Darlington) which also interprets the chiasma frequency in short and long chromosomes and chromosome arms, because quadrivalents result from chiasma formation in the paired segments of all four homologous chromosomes, presented in the autotetraploids. Most of the autotetraploids also form trivalents and univalents, parallel with bivalents and quadrivalents. Abnormal distribution of the univalents and the members of the trivalent and quadrivalent groups during the meiosis is one of the most essential causes for the reduction of fertility in autotetraploids and for their survival, because they lead to formation of disbalanced (in respect to the chromosome numbers) gametes. (A relative reduction of the velocity of the pollen tube growth especially of the disbalanced gametes is another factor that conditions reduced fertility.)

The degree of fertility is the most essential factor, that regulates the survival of the new tetraploid.

Allotetraploids, derived from $F_1$-hybrids with asyndetic meiosis (*I*) usually have normal meiosis (forming only bivalents, rarely univalents) and are highly fertile. Allotetraploids derived from $F_1$-hybrids with complete allosyndetic meiosis (*II*) behave very much like the autotetraploids forming bivalents, quadrivalents, trivalents and univalents and usually have, like them, somewhat (or highly) reduced fertility. Allopolyploids derived from $F_1$-hybrids with partial allosyndesis during the meiosis (*III*) occupy a position between the two extremes (*I*) and (*II*).

On the basis of the preceding statements we can logically deduce that autopolyploid forms derived from species with short chromosomes should survive better in nature, because they form more bivalents and less quadrivalents (trivalents too), than those derived from species with long chromosomes. Allotetraploids derived from $F_1$-hybrids with allosyndesis should behave in a similar way. Consequently, polyploid species in nature with long chromosomes of a higher degree of polyploidy would have most frequently an allopolyploid origin; $F_1$-hybrids from which such species have been derived should have, most probably, asyndetic meiosis or only partial allosyndesis. There is a relatively small chance for the survival of autotetraploid forms derived from species with long chromosomes and of allotetraploids with long chromosomes, derived from

$F_1$-hybrids with normal or high allosyndesis during the meiosis. Studying a series of polyploid forms existing in nature and experimentally produced, as well as the drawings of chromosomes in diploids and polyploids, made by other investigators, I obtained data which support strongly these deductions. Autopolyploid forms, with largest chromosome numbers found in nature are derived from species with small chromosomes. Such forms are, for example, *Silene ciliata* Pourr. with $2n = 24$, 48 and 192 chromosomes, *Dianthus sinensis* L. (*Seguieri* Vill.) with $2n = 60$ and 90 (*Dianthus superbus* L., — *arenarius* L., having $2n = 30$ and 60) chromosomes, etc. (*cf.* the list of the autopolyploids given by Müntzing[16]).

Autopolyploidy induced in plants with long chromosomes leads to high or complete sterility. *Triticum vulgare* autotetraploids[17,18] ($2n = 84$) produced by abnormal temperatures were self-sterile. Auto-octoploid *Tr. durum*, which I grew, was also self-sterile. Genus *Nicotiana* has much shorter chromosomes than *Triticum*. Autotetraploids *N. alata* ($2n = 36$) and *N. longiflora* ($2n = 40$), which I produced, by colchicine and acenaphthene were highly fertile, while the octoploid *N. alata* ($2n = 72$) was self-sterile. In other words, high polyploidy also reduces fertility.

I shall further consider a series of plants in which the species with large chromosome numbers have small chromosomes. Smith[19] (1937) studied the chromosome numbers in *Dioscoreaceæ*. His drawings show that *Dioscorea caucasica* ($2n = 20$) and *D. quinqueloba* ($2n = 20$) have large chromosomes, the species *D. reticulata* ($2n = 61$) and an undefined sp. ($2n = 40$) have medium chromosomes, while *D. batatas* ($2n = 144$) has small chromosomes. Similar regularity can be found in studying the drawings made by Baldwin[20] (1936) of the *Crassula* karyotypes. The species of the division *Turrita*, namely, *Crassula barbata* ($2n = 14$) and *C. hemispherica* ($2n = 14$) have large chromosomes, while *C. nodulosa* ($2n = 56$) has medium chromosomes. The species from other divisions, namely, *Crassula sarmentosa* ($2n = ca.\ 60$), *C. multicava* ($2n = ca.\ 112$) and *C. spatulata* ($2n = ca.\ 148$) have short chromosomes. The species of the genus *Griffinia* studied by Satô[20a] also represents an excellent example in this respect. In genus *Sedum*[21] no noticeable difference exists in the chromosome length of the species with small and with large chromosome numbers, they all have, however, short chromosomes. The chromosomes of diploid *Lobelia* species (*inflata, syphilitica, dresidensis*, $2n = 14$), as drawn by Okuno[22] (1937), have large chromosomes, tetraploid species *L. sessilifolia* ($2n = 28$) has medium chromosomes, and hexaploid species *L. Richardsonii, triquetra* and *Erinus* ($2n = 42$) have small chromosomes. *Geranium erianthum* ($2n = 30$) has long chromosomes, *G. Sanguineum* ($2n = 84$) has short chromosomes as the drawings of Sakai[23] (1935) showed. His[24] drawings also showed that diploid *Aconitum* species (*umbrosum* and *yuparense*, $2n = 16$) have longer and thicker chromosomes than tetraploid *A. sachalinense* ($2n = 32$) and *A. subcuneatum* ($2n = 32$). The drawings of Tanaka[25] (1937) showed that *Scirpus mucronatus* ($2n = 42$) has the largest chromosomes, *S. cyperinus* var. Wichurai ($2n = 66$) has medium and *S. Maritimus* ($2n = 110$)—the smallest chromosomes. But, in general, genus *Scirpus* has small chromosomes in comparison with *Triticum*, for example. Strekova[26] (1938) studied and drew the chromosomes of the genus *Alopecuros* (*A. æqualis*, $2n = 14$; *A. ventricosus*, $2n = 28$; *A. glacialis*, $2n = 56$; *A. borealis*, $2n = 98$). According to her drawings, *A. æqualis* ($2n = 14$) has the largest and the thickest chromosomes, while *A. borealis* ($2n = 98$)—the smallest and the thinnest. Delaunay[27] (1926) studied the chromosome number and size of *Muscari, Bellevalia* and *Ornithogalum* and found that species with smaller chromosome numbers have usually longer chromosomes, attempting at the same time to evaluate this statement, phylogenetically, though in a different aspect. Examining numerous drawings of the karyotypes of a large number of species of phanerogamous plants made by Matsuura and Sutô[28] (1935), one feels easily convinced that species with gigantic chromosomes have not large chromosome numbers. Such species are: *Hepatica triloba* ($n = 7$), *Anemone flaccida* ($n = 7$), *Diphylleia Grayi* ($n = 6$), *Trautvetteria japonica* ($n = 8$), *Achlys japonica* ($n = 6$), *Sironema fragrans* ($n = 6$), *Hyacinthus orientalis* ($n = 8$), *Disporum sessile* ($n = 8$), *Aloe* sp. ($n = 7$), *Gesteria* sp. ($n = 7$), *Howarthia* sp. ($n = 7$), etc. It should be noted that all species of *Howarthia*[29, 30] hitherto studied are diploids ($2n = 14$). No polyploid *Lilium* species have been yet found, the whole genus having long ($n = 12$) chromosomes. Genus *Dianthus*, on the other

hand, has very small chromosomes and according to the data of Blackburn and those of Rohweder (*cf. Tischler,*[31] 1931) 25 species have $2n = 30$ chromosomes, 9 species have $2n = 60$ chromosomes and 11 species have $2n = 90$ chromosomes. The species *D. plumarius* has $2n = 30$ and 90 (Rohweder) and species *D. prolifer* has $2n = 30$ and 60 chromosomes. *Betula*[32] and *Populus*[33] have small chromosomes; *Betula* species having $2n = 28$, 56, 84 and even 90 chromosomes, and *Populus* species: $2n = 38$ and 57 chromosomes. The species *Betula japonica* has $2n = 28$ and 56 chromosomes. *Fragaria, Viola* and *Campanula* species also have relatively small chromosomes. *Fragaria*[31] has a polyploid series between $2n = 14$ and 84. The smallest chromosome number in *Viola* is $2n = 12$, the largest $2n = 96$. The species of the genus *Campanula*[31] have $2n = 16$, 32, 34 and 102 chromosomes. In *Gramineæ* there are genera with long chromosomes (*Triticum,* $2n = 14$, 28, 42; *Secale,* $2n = 14$; *Ægilops* $2n = 14$, 28, 42, etc.) and genera with shorter chromosomes (*Leersia,*[34] *Ehrharta,*[35] *Saccharum,*[36,37] *Setaria,* etc.). *Secale* species are only diploid. The polyploid species of *Triticum* and *Ægilops* have $2n = 28$ and 42 chromosomes, all of them being allopolyploids. New allopolyploid forms with $2n = 56$ have been experimentally produced, but they usually have somewhat reduced fertility. In the genus *Leersia*[34] on the other hand, the following chromosome numbers were reported by Hirayoshi[34] (1937): $2n = 48$ (*L. hexandra*), $2n = 60$ (*L. oryzoides* and $2n = 96$ (*L. japonica*). In *Saccharum,* species with $2n = 60$, 80 and with 112 (*S. spontaneum*) chromosomes have been reported by Bremer. *Setaria* species have $2n = 18$, 36 and 72 chromosomes (Kishimoto, 1938). The species *Agropyrum elongatum* ($2n = 70$) has relatively long chromosomes and, at the same time, a large chromosome number. The cytogenetic investigations showed, however, that this decaploid species is most probably allopolyploid, at least in respect to four genoms, only one being perhaps presented twice; the most reliable genom formula of it being AA BB CC $X_1X_1$ $X_2X_2$. *Narcissus dubius* ($2n = 50$) represents a similar case. It has the largest chromosome number of this genus. All *Narcissus* species have long chromosomes. Cytogenetic studies by Fernandes[39] (1937) showed that this species is an auto-allopolyploid having two genoms of *N. juncifolius* ($2n = 14$) and one genom of *N. tazetta* ($n = 11$), the genom formula of *N. dubius* being $\frac{JJT}{JJT}$. Cytogenetic studies also showed that *Helianthus*[38] *tuberosus* ($2n = 102$) is most probably an allo-autopolyploid having a genom formula $\frac{At_1\ At_2\ Bt}{At_1\ At_2\ Bt}$, the genom Bt being closely related to *Helianthus annuus* ($2n = 34$) genom. But *H. tuberosus* still has abnormalities during the meiosis and reduced fertility. If this species does not propagate vegetatively it hardly would survive. It has medium chromosomes.

The mode of propagations (vivipary) seems also to "protect" high polyploidy in some alpine and arctic plants (grasses). It seems that low temperatures (especially at night) favour polyploidy. At low temperature the chromosomes become shorter thus offering smaller segments for conjugation and for chiasma formation. Cold reduces pairing and chiasma formation. This is most probably due to an increase in the cytoplasmic viscosity and shortening of the chromosomes.

I shall also consider here the long list of chromosome numbers recorded by Sutô[40] (1936) in *Liliaceæ* and *Amaryllidaceæ*. It is not very suitable for our studies because no drawings were given, but nevertheless, he classified the karyotypes into four groups which fit generally quite well to the general principles here outlined. Idiograms of the type *Yucca—Agave* (4–5 long + *n* dots) were designated YA; further TD = *Tofieldia—dracœna* (*n* dots); LN = *Lilium—Narcissus* (*n* longs); and UP = *Uvularia—Polygonatum* (*m* longs + *n* dots). Species with large chromosome numbers have most frequently idiograms TD and YA (*Hosta, Drimiopsis, Yucca, Cordyline, Dracœna, Sanseviera, Agave, Fourcroya, Beschorneria, Polyanthus*).

One can also conclude from the drawings made by Hagerup[41] (1938) that there are species in genus *Orchis* with large (*O. maculatus* var. *Meyeri,* $2n = 40$; *O. ustulatus,* $2n = 42$) and such with small chromosomes (*O. purpureus,* $2n = 42$; *O. sambucinus,* $2n = 42$; *O. incarnatus,* $2n = 40$). The polyploid forms, *O. latifolius* ($2n = 80$) and *O. maculatus* var. *genuinus* ($2n = 80$), however, have small chromosomes. The case with *O. maculatus* shows that a crowding of the chromosomes in the polyploid form is connected with somewhat smaller size of the chromosomes. Such a conclusion

might be premature, especially when it is drawn from polar views of meiotic chromosomes. Examining, however, the size of the somatic chromosomes of diploid *Artemisia borealis* ($2n = 18$) in respect of those of the tetraploid variety *bottnica* ($2n = 36$) drawn by Erlandsson[42] (1939), I think that such a tendency does exist. Variety *bottnica* has somewhat smaller chromosomes. In comparing the chromosome size of diploid and octoploid *Nicotiana alata*, I had the same impression, namely, that the octoploid species had somewhat thinner and shorter chromosomes than the diploid one. There is a very striking difference in the chromosome size between those of *Plantago lanceolata* var. *altissima* from Bucharest ($2n = 12$) and those of *P. lanceolata* var. *altissima* from Munich ($2n = 96$), studied by McCullagh,[43] the chromosomes of the diploid form ($2n = 12$) being about 4 or 5 times larger in size than those of the *16-ploid*.

It seems that hydration (viscosity degrees) and nutrition processes (*i.e.*, differences in amount of substances, present in the nucleus, resp. passing through the nuclear membrane, necessary for chromosome growth and reproduction in polyploid large nuclei, where the chromosomes are more crowded in comparison with those of the diploids, where they are less crowded) are responsible for these differences in degree. It should be pointed out here that smaller nuclei, typical for the diploids, can be better supplied by the cytoplasm with substances necessary for the growth and reproduction of the chromosomes than the large polyploid nuclei, since the former nuclei have larger surface in relation to their volume than the latter. The decrease of the ratio $\frac{\text{nucleus surface}}{\text{nucleus volume}}$ with the euploid increase of the chromosome numbers is probably the main factor that suppresses the frequency of the cell division in high polyploids. Octoploid *Nicotiana alata* ($2n = 72$), for example, has larger nuclei and larger cells than the tetraploid ($2n = 36$) and diploid ($2n = 18$) *N. alata*, it was, however, smaller in size, *i.e.*, it had much smaller number of cells. Our more recent observations also suggest that the decrease in the $\frac{\text{nucleus surface}}{\text{nucleus volume}}$ ratio with the euploid increase of the chromosomes in plants regulates the change in the leaf index (a decrease of $\frac{\text{length of the leaves}}{\text{breadth of the leaves}}$ with the euploid increase of the chromosomes).

In the trend of this discussion I shall call attention to the better survival of polyploids than of diploids with some chromosome deficiencies (deletions), which also lead to differentiation of karyotypes with some shortened chromosomes. This process might often occur during the chromosome differentiation (genic and structural) of the newly raised polyploids until they change from plants with multivalent chromosomes during the meiosis into plants with bivalent chromosomes.

Some cytogenetic data suggest that the chromosome size is under genic control.[4] It does not seem improbable, that some polyploids have survived, because they are mutants with short chromosomes. A too great crowding of chromosomes in polyploids of higher degree, especially when the latter are large and even medium in size also interferes with the meiotic processes. Autotetraploids *Nicotiana alata* ($2n = 36$) and *N. longiflora* ($2n = 40$), for example, have a much normal meiosis and higher fertility than the autotetraploid forms of *N. rustica* ($2n = 96$) varieties. The latter varieties set only on the average 10 to 25% of seeds. It should be pointed out that *N. rustica* is an allopolyploid species its haploid forming usually 0-1 bivalents. One of the essential factors for the reduction of fertility in high polyploids is obviously the reduction of the ratio $\frac{\text{average diameter of the pollen mother cells}}{\text{average diameter of the meiotic equatorial plates}}$ with the euploid increase of the chromosomes. This ratio for *N. rustica* diploid is 1·783 and for *N. rustica* tetraploid —1·496. Another important factor that is responsible for some abnormalities during the meiosis is the size of the leptotene nuclei. High polyploids are more likely to form less quadrivalents (proportionally) and more univalents, because the chromosome pairing attraction should be inversely proportional to the square of the distance between the chromosomes at leptotene. If two homologous chromosomes occupy diametrically opposite positions in a very large polyploid nucleus, their pairing attraction might be so reduced that they may fail to pair. It seems quite logical that the crowding itself of the chromosomes in polyploids with large chromosome numbers would reduce pairing and chiasma formation. Insignificant external conditions that interfere with the meiotic processes (temperature, viruses, etc.) would induce in such high polyploids greater meiotic disturbances than in plants with smaller nuclei.

Preceding considerations of the significance of chromosome size and number are of importance from a practical point of view. It might be suggested that polyploids (especially autopolyploids) when produced for practical purposes should be better derived (when possible) from plants with smaller chromosomes (in size) and with smaller chromosome numbers.

---


[1] Winge, O., *C. R. Carlsb. Lab.*, 1917, **13**, 131–275.

[2] Kostoff, D., *Curr. Sci.*, 1938, **7**, 108–10 ; *Nature*, **142**, 753, 1117.

[3] Darlington, C. D., *Cytologia*, 1930, **2**, 37–55 ; 1933, **4**, 444–52.

[4] ————, *Recent Advances in Cytology*, 1932, 1937, I and II Ed., London.

[5] Mæda, T., *Mem. Coll. Sci. Kyoto Imp. Univ.*, 1930, **5**, 125–37.

[6] Stone, L. H., and Mather, K., *Cytologia*, 1932, **4**, 16–25.

[7] Sax, K., *ibid.*, **1**, 35 ; **6**, 289–93.

[8] Drummond, F. H., *ibid.*, 1938, **8**, 343–52.

[9] Bennett, E. S., *ibid.*, 1938, **8**, 443–51.

[10] Darlington, C. D., *Biol. Bull.*, 1932, **63**, 357–67, 368–71.

[11] ————, and Dark, S. O. S., *Cytologia*, 1932, **3**, 169–85.

[12] Satô, D., *Bot. Magaz.* (Tokyo), 1934, **48**, 823–46.

[13] White, M. J. D., *Cytologia*, 1933, **5**, 135–39.

[14] Klingstedt, H., *Mem. Soc. Fauna Flora Fenn.*, 1937, **12**, 194–209.

[15] Kostoff, D., unpublished.

[16] Müntzing, A., *Hereditas*, 1936, **21**, 263–378.

[17] Dorsey, E., *Jour. Hered.*, 1936, **27**, 154–60.

[18] Peto, F. H., *Canad. Jour. Res. C.*, 1938, **16**, 516–19.

[19] Smith, B. W., *Bull. Torrey Bot. Club*, 1937, **64**, 189–97.

[20] Baldwin, J. T., *Jour. Genet.*, 1936, **33**, 455–63.

[20a] Satô, D., *Cytologia*, 1938, **9**, 203–42.

[21] Baldwin, J. T., *Amer. Jour. Bot.*, 1937, **24**, 126–32.

[22] Okuno, S., *Cytologia*, Fujii Jub. Vol., pp. 897–902.

[23] Sakai, K., *Jap. Jour. Genet.*, 1935, **11**, 68–73.

[24] ————, *Trans. Sappore Nat. His. Soc.*, 1933, **8**, 74–77.

[25] Tanaka, N., *Cytologia*, Fujii Jub. Vol., 1937, pp. 814–21.

[26] Strelkova, O., *Cytologia*, 1938, **8**, 468–80.

[27] Delaunay, L. N., *Zeit. f. Zellforsch. und mikr. Anat.*, 1926, **4**, 338–64.

[28] Matsuura, H., and Sutô, T., *Journ. Fac. Sci., Hokkaido Imp. Univ., Ser. V*, 1935, **5**, No. 1, 33–75.

[29] Taylor, W. R., *Amer. Jour. Bot.*, 1925, **12**, 219–22.

[30] Ferguson, N., *Roy. Soc., London, Phil. Trans.*, (B), 1926, **215**, 225–53.

[31] Tischler, G., *Tabulæ Biol.*, 1931, **7**, 109–226.

[32] Woodworth, R. H., *Bot. Gaz.*, 1929, **87**, 331.

[33] Peto, F. H., *Canad. Jour. Res. C.*, 1938, **16**, 445–55.

[34] Hirayoschi, I., *Jap. Jour. Genet.*, 1937, **13**, 215–16.

[35] Parthasarathy, N., *Ann. Bot.*, N.S., 1939, **3**, 43–76.

[36] Bremer, G., *Arch. Suiker. Ind. Nederland Ind.*, 1924, **16**, 477.

[37] Bremer, G., *Rec. trav. Botan. Néerl.*, 1928, **25a**, 82.

[38] Kostoff, D., *Genetica*, 1939 (in the Press).

[39] Fernandes, A., *Bull. Soc. Boter.*, Ser. II, 1937, **12**, 93–116.

[40] Sutô, T., *Jap. Jour. Genet.*, 1936, **12**, 107–12.

[41] Hagerup, O., *Hereditas*, 1938, **24**, 258–64.

[42] Erlandsson, S., *ibid.*, 1939, **25**, 27–30.

[43] McCullagh, D., *Genetica*, 1934, **16**, 1–44.


---

## Professor J. C. Ghosh, D.Sc., F.I.C., F.N.I.

*(Director, Indian Institute of Science, Bangalore)*

THE news of the appointment of Professor J. C. Ghosh as Director of the Indian Institute of Science will, we are confident, be received with generous enthusiasm both in India and abroad, and we have pleasure in offering him our warmest felicitations on his elevation to what we regard as the Pontifical Chair in the realm of Indian Science. It will be recalled that as the Head of the Department of Chemistry in the Dacca University, his strenuous labours have established a flourishing school of chemical research, whose contributions have as much significance in the field of theoretical knowledge as they have important practical applications in industry. Professor Ghosh's achievements have brought him blushing honours, thickly and surely. He was one of the organising members of the Indian Chemical Society of which he became