Cytogenetical Studies in *Avena*. III Experimentally produced eu- and hyperhexaploid aberrants in oats *

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As stated in the preceding paper, pentaploid *Avena* hybrids were karyologically unbalanced and gave rise to alternations of chromosome combination in the offspring. Out of many segregates with these new chromosome combinations, three constant strains were established in later selfed and back crossed progenies of the hybrid between *Avena fatua* ($n = 21$) and *A. barbata* ($n = 14$). Two strains showed 21 pairs of chromosomes at meiosis and the remaining one 22 pairs (NISHIYAMA 1939).

In the present account is given chiefly a further study on the qualitative analysis of the chromosome complement in these constant forms.

In external morphology these new forms approached *A. fatua*, but showed many minor distinctions from it and among themselves. Before describing the cytological observation, therefore, their morphological characteristics will be briefly indicated.

Morphology of *A. fatua*: Culms semi-erect in early growth period, 127 cm long, ears equilateral, wide spreading, drooping, 80 spikelets, basilar articulation distinct, all florets readily separating from their axes in ripening, basal hairs present in bushy ring, empty glume ca. 22 mm long, lemma dark brown, covered with long hairs, awns twisted and geniculated (cited from NISHIYAMA 1929).

In the three strains, principal characters which are distinct from *A. fatua* are as follows:

Pc-1 (BF_2 with 21 bivalents in Table 4, NISHIYAMA 1939); culms nearly normal height, 110 cm, lemma (or grain) somewhat longer, brown, ca. 74 spikelets per panicle.

Pc-2 (BF_4 with 21 bivalents in Table 4, NISHIYAMA 1939); Semi-dwarf, i.e. culms ca. 75 cm long, grain and awns somewhat longer, lemma brown, empty glume longer but narrower, ca. 36 spikelets per panicle.

Pc-3 (BF_4 with 22 bivalents in Table 4, NISHIYAMA 1939); Semi-dwarf, i.e. culms 70 cm long, grain somewhat smaller, blackish

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brown like *A. barbata*, lemma of the first grain carries a small number of short hairs, the second grain usually glabrous, empty glume longer but narrower, ca. 40 spikelets per panicle.

The fertility of these new forms is usually normal, but is often variable, probably being influenced by environmental condition at the time of flowering.

Among the three strains and *A. fatua*, all of six possible crosses were made and F_1 hybrids were used for the study on the meiotic pairing of chromosomes. The cytological results are summarized in the following scheme. That is, it means that the hybrid between Pc-1 ($n = 21$) and *A. fatua* ($n = 21$) shows twenty-one chromosomes closely paired at first metaphase in PMC, and so on (Fig. 1a).

Scheme showing chromosome affinity in the hybrids among four oat strains.

In Pc-2 ($n = 21$) $\times$ *A. fatua* ($n = 21$) twenty bivalent chromosomes are formed in a normal manner but the remaining two show no tendency toward pairing. Similar chromosome pairing is also found in Pc-3 ($n = 22$) $\times$ *A. fatua* ($n = 21$) but in this case one extra chromosome of the former is also left unpaired. Accordingly, this hybrid always

exhibits $20n + 3t$ at first metaphase (Fig. 1c). In Pc-3 ($n = 22$) $\times$ Pc-2 ($n = 21$), the chromosome configuration is usually $21n + 1t$ and in rare cases $20n + 3t$. From these facts it probably may be said that both of these strains have a similar chromosome complement, with the exception of one extra chromosome of Pc-3. The chromosome pairing $20n + 2t$, in the hybrid, Pc-1 ($n = 21$) $\times$ Pc-2 ($n = 21$), and $20n + 3t$ in Pc-1 ($n = 21$) $\times$ Pc-3 ($n = 22$) may readily be understood from the facts mentioned just above (Fig. 1b).

Judging from their size and shape, showing a median or sub-median constriction, two univalents from the hybrids with $20n + 3t$ appear always to correspond with those of the hybrids with $20n + 2t$. The third univalent of the former has also a median constriction, but is the smallest. From these facts it seems probable that in these hybrids certain specific chromosomes always fail to pair.

These cytological evidences suggest strongly that Pc-2 has a reconstruction complement of chromosomes, containing twenty pairs of *fatua* chromosomes and one pair of *barbata* chromosomes which is unable to conjugate with any of the *fatua* chromosomes. Pc-3

also possesses the same complement as Pc-2 and one pair of specific *barbata* chromosome in excess. In the last strain, Pc-1, the chromosome situation appears to be completely homologous with that of *A. fatua*.

Fig. 1. Chromosomes at first metaphase in PMC. a, Pc-1 $\times$ *A. fatua*, 21_{II} ; b, Pc-1 $\times$ Pc-2, $20_{II} + 2_I$; c, Pc-3 $\times$ *A. fatua*, $20_{II} + 3_I$.

The genome formula of *A. fatua* and *A. barbata* was shown by the symbol AAB $\overline{B}$ CC and AAB'B' respectively (NISHIYAMA 1934, 1939). If we assume that the B genome contains $b_1b_2b_3b_4b_5b_6b_7$ chromosomes, *A. fatua* and Pc-1 might be represented by the formula $AACC + 2 \times b_1b_2b_3b_4b_5b_6b_7$. While Pc-2 would be shown by $AACC + 2 \times b_2b_3b_4b_5b_6b_7 + 2\beta_1$ and Pc-3 by $AACC + 2 \times b_2b_3b_4b_5b_6b_7 + 2\beta_1 + 2\beta_2$ in which β_1 and β_2 are specific *barbata* chromosomes.

Although these new forms markedly resemble *A. fatua*, in some external characters they are like *A. barbata* or distinct from either of the parental species. The origin of these new or *barbata*-like characters would probably be assumed to be partly due to the reconstruction of the chromosome complement referred to above and partly due to the replacement of some *fatua* chromosomes by *barbata* homologues (cf. NISHIYAMA 1934). According to NISHIYAMA (1929) it has already been found that the maximum number of paired chromosomes amounted to 11 in the hybrid between *A. barbata* and *A. fatua*. This cytological fact might support the possible occurrence of such a chromosomal exchange between the two species without any cytological disturbance.

There have been reported some similar cases in which new hyperpolyploid forms are experimentally produced. COLLINS, HOLLINGSHEAD and AVERY (1929) found a new species *Crepis articialis* ($n = 12$) from the interspecific hybrid *C. biennis* ($n = 20$) $\times$ *C. setosa* ($n = 4$). Its chromosome complement consisted of ten pairs

from *biennis* and two pairs of *setosa* chromosomes. WEBBER (1930) obtained a distinct new type with twenty-five bivalents from the offspring of the sesquidiploid *Nicotiana* hybrid which probably had arisen from the union of a diploid *tabacum* egg and a haploid *sylvestris* sperm. Later LAMMERTS (1932) also established a new strains having $n = 24$ *rustica* + 6 *paniculata* chromosomes by selfing the back cross hybrid [*Nicotiana rustica* ($n = 24$) $\times$ *paniculata* ($n = 12$)] $\times$ *rustica* ($n = 24$). Finally it was shown by UCHIKAWA (1937) that the short *compactum* type contained twenty-two bivalents from which one bivalent was reduplicated in excess as compared with normal *vulgare* wheat ($n = 21$).

A similar chromosome situation as in Pc-2 has already been found by KIHARA and WAKAKUWA (1935) in giant types which arose spontaneously from dwarf wheat with twenty bivalents. These giant wheats were clearly euhexaploid as usual but had nineteen different and two duplicated pairs of chromosomes.

Since these aberrants have new chromosome complements as well as new and different plant characters they might be considered as new varieties or might require more distinctive taxonomic recognition.

In short, the present work provides a further example of the induction of aberrants with quantitatively and qualitatively altered complements of chromosomes which are due to the recombination of chromosomes from two distinct plant species.

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