CHAPTER 14

# The Aneuploids

## 14.1: Aneuploids Among the Treated Generation

The variations in numbers of chromosomes through loss or gain of extras were first appreciated for their possible value in fundamental cytogenetics by Belling and Newton.[26] Since then the aneuploids have been accumulating in large numbers for many genera. A new group of aneuploids was developed when colchicine was used with large populations of treated plants. Certain plants were deficient for a chromosome, and among the diploid species these losses were very rare but significant.[6] All diploid deficient types, including the $2n - 1$ *Datura stramonium* plants, failed to set seed. The origin of such types is an interesting problem, for the action of colchicine must be interpreted somewhat differently from the usual doubling of chromosomes.[4] Apparently a mitotic disturbance, the loss of a chromosome at the time of treatment, is transmitted through mitotic processes until meiosis, when these types are discovered.

That diploid deficient plants are rare is emphasized when we learn that only 55 spontaneously occurring 23-chromosomal types ($2n - 1$) have been recorded from among more than 2 million *Datura* plants recorded over a period of years.[6] From a standard line *l* of *Datura,* the frequency of a $2n - 1$ plant is 1 out of 20,879 offspring, compared with 7 such types found among 2135 plants growing from treated cultures.[6] The frequencies are increased by colchicine more than 70 times over the naturally occurring rate. Since the records were made from pollen mother cells, only the diploid deficiencies from the subepidermal layer that fell in the germ line were calculated. Therefore, the incidence of $2n - 1$ tissues created by colchicine was higher than these figures show.

Out of 88 plants in the deficient class, 81 were tetraploid deficient kinds, i.e., $4n - 1$ or $4n - 1 - 1$. Similar to the diploid deficient plants, the tetraploid deficient cases arose from the effects of colchicine.[4]

One other fact is striking. There were, in all, 173 chromosomes lost; and the largest type, known as the *L* chromosome, was missing more often than other types. Previous data for spontaneously occurring *Datura* showed that the $1 + 2$, or *L* chromosome was missing more often than any other type. Special morphological traits are fairly reliable for recording *Datura* progenies.[4]

Before these data were reported, missing chromosomes were known in *Drosophila*. *Nicotiana*[48] heteroploids were obtained by other treatments, and a genetic demonstration proved the loss of chromosomes in a culture of *Hyocyamus niger*. Since the *Datura* work was published, deficient types have been recognized in *Nicotiana*,[48] *Lilium*,[20] and *Eruca*.[39] There must be many that have escaped notice and also records that are not specifically listed here.

If one looks at the recovery stages from colchicine, the explanation for the tetraploid deficient types can be seen easily. One or two chromosomes are left outside the restitution tetraploid nucleus. The causes of a diploid deficient case require additional examination because a c-mitosis leading to a tetraploid restitution nucleus would not have taken place unless a distributed c-mitosis of unequal distribution, 23 and 25 respectively, occurred. The 23-chromosome cell would lead to a deficient cell and the 25 to extra-chromosome types. There is yet another explanation. When grasshopper neuroblasts were treated at certain concentrations that did not completely destroy the spindle, certain chromosomes were lagging. Presumably an incomplete inhibition could cause one chromosome to lag. The fact that the largest chromosome of *Datura* was the one most often missing is of interest.[4] To assume that tetraploid deficient types and the diploid deficiencies arose from a similar action on the spindle appears to be oversimplification of the problem.

Among the progenies of these treated plants there appeared also extra-chromosomal types.[4] The fifteen-year breeding record for *Datura* showed that $0.16 + .019$ per cent of the $2n$ plants recorded were extra-chromosomal types.[6] Among the 2135 plants, $0.52 + .105$ per cent had one or more chromosomes. This value is 3.36 times the probable error, and combining data for two years leads to a value 4.42 times the probable error.[4] An increase caused by colchicine seems a reasonable explanation. Of the extra-chromosomal types induced by colchicine, ten plants had $2n + 1$ chromosomes, one had $2n + 1 + 1$, and three were $4n + 1$. If colchicine increased the frequency, the action had to occur at mitosis during treatment. A specific action on the spindle directed to one chromosome is suggested.

Aneuploids from treatments in *Lilium longiflorum* were analyzed from root tips and not the pollen mother cells.[20] Out of 500 plants treated and analyzed, 303 cases from roots were counted. Eight aneu-

ploids were found; these were either $4n$ deficient or $4n$ plus one chromosome.[20] Among heteroploids in *Nicotiana,* deficient types ($2n - 1$) like those in *Datura* were found. Similarly, in *Eruca sativa* the plant was lacking two chromosomes, $2n - 2$. No explanation different from that advanced for *Datura* has been made. The deviation originated when colchicine acted on somatic mitosis.

In view of these cases we are prompted to suggest that the subtype of exploded c-metaphase, the distributed c-metaphase, should be studied further with respect to unequal distributions of chromosomes following treatment with colchicine. Activity of this type was often observed in pollen tubes of *Polygonatum*, but the relation to such phenomena has been for the most part overlooked. As a basis for an action of colchicine on mitosis that leads to numbers other than the true polyploids, illustrations are abundant in cultures of pollen tubes which account for a variety of deviating numbers that might occur when colchicine acts on mitosis.

### 14.2: Mixoploidy From Colchicine

The action of colchicine upon individual cells was emphasized in the first studies with *Allium* roots. A single root tip treated for 72 hours may yield cells with many chromosomes while other cells remain diploid. It has been confirmed many times that within one meristematic group there may remain diploid cells alongside tetraploids. Such tissues are described as mixoploid. These cases should not be confused with sectorial chimeras since the word means *mixed together.*

A cyto-histological study of maize after treatment with colchicine showed that different areas may become tetraploid more readily than others.[41] Treatment of maize plants with colchicine rarely gives rise to a completely tetraploid plant.[41] Certain branches of the tassel show tetraploid, and others, diploid pollen. Whether these are true sectorial chimeras or the result of mixoploid conditions has not been decided.

Another case of mixoploid tissues from treated plants was followed through enough generations to prove that mixoploids were involved rather than sectorial chimeras.[24] *Lolium perenne* L., $2n = 14$, was originally treated by subjecting seed to colchicine.[24] Plants with tetraploid cells, determined by measurements of pollen grains and chromosomal counts in root tips, were isolated. Supposedly tetraploid tillers were being separated and transplanted. Also some clones were separated as progenitors for control diploid clones. Selections were again made for diploid and tetraploid clones.[24] As before, chromosomes were counted. For two generations such propagation was continued, yet mixoploid tissues persisted into the seventh gen-

eration of vegetative propagation in spite of well planned and carefully followed methods of determining numbers of chromosomes. These seven generations were preceded by four vegetative generations in which two were selected after chromosomes were determined to guide the selection.

In some cases individual anthers yielded diploid and tetraploid microspore mother cells.[20] Clearly a mixoploid tissue gave rise to these anthers. Remembering that tested plants were removed from the tetraploid progenitors by several generations of propagation, the persistence of diploid and tetraploid cells with neither one crowding out the other is of particular interest. *Lilium* is considered to be tetraploid on the basis of chromosome counts; yet diploid and tetraploid pollen mother cells have been found in the same anther of lilies.[20] In one test a generation was grown by scale propagation and ten plants were selected. One plant from scale propagation and three plants obtained by dividing the original bulb yielded flowers with anthers that had both diploid and tetraploid cells. The parent plant was supposedly a tetraploid.

Both cases mentioned here, *Lilium* and *Lolium*, represent vegetative propagations, and in each instance colchicine created a mixoploid tissue. Projects that involve vegetative increase present complex problems, the true nature of which remains unsolved.

### 14.3: Chimeras Induced by Colchicine

In longitudinal section, the apical meristem of *Vinca rosea* L. shows a distinct layering of cells.[14] These are clearly illustrated with the photomicrograph in Figure 14.1, *A* and *B*. Using terminology promoted by plant anatomists, the first layer is called $T_1$ and the next $T_2$. These, then, refer to the first and second layers of a *tunica*. The third layer and cells deeper in the apex are called the *corpus*, initialed $C_1$ and $C_2$. Lower than $C_2$ no specific layers can be observed.[14]

From species to species the limits of the tunica and corpus may vary. For example, *Vinca minor* L., obviously related to *V. rosea*, was described with three layers of tunica and a fourth as the corpus. If the older terminology of Hanstein is related to the tunica-corpus concept using *Vinca minor* as an example, then $T_1$ is equivalent to Hanstein's dermatogen, $T_2$ and $T_3$ are the same as periblem, and $C_1$ is the plerome. Another and different labeling has been used in recent cyto-chimeral studies following polyploidy induced by colchicine. The layers are called *L*-I, *L*-II, and *L*-III, etc. without reference to a tunica and corpus.[14]

The point to be strongly emphasized here is not the terminology but the fact that the various layers make a definite and precise contribution to the shoot axis and to such parts of shoot as the flower

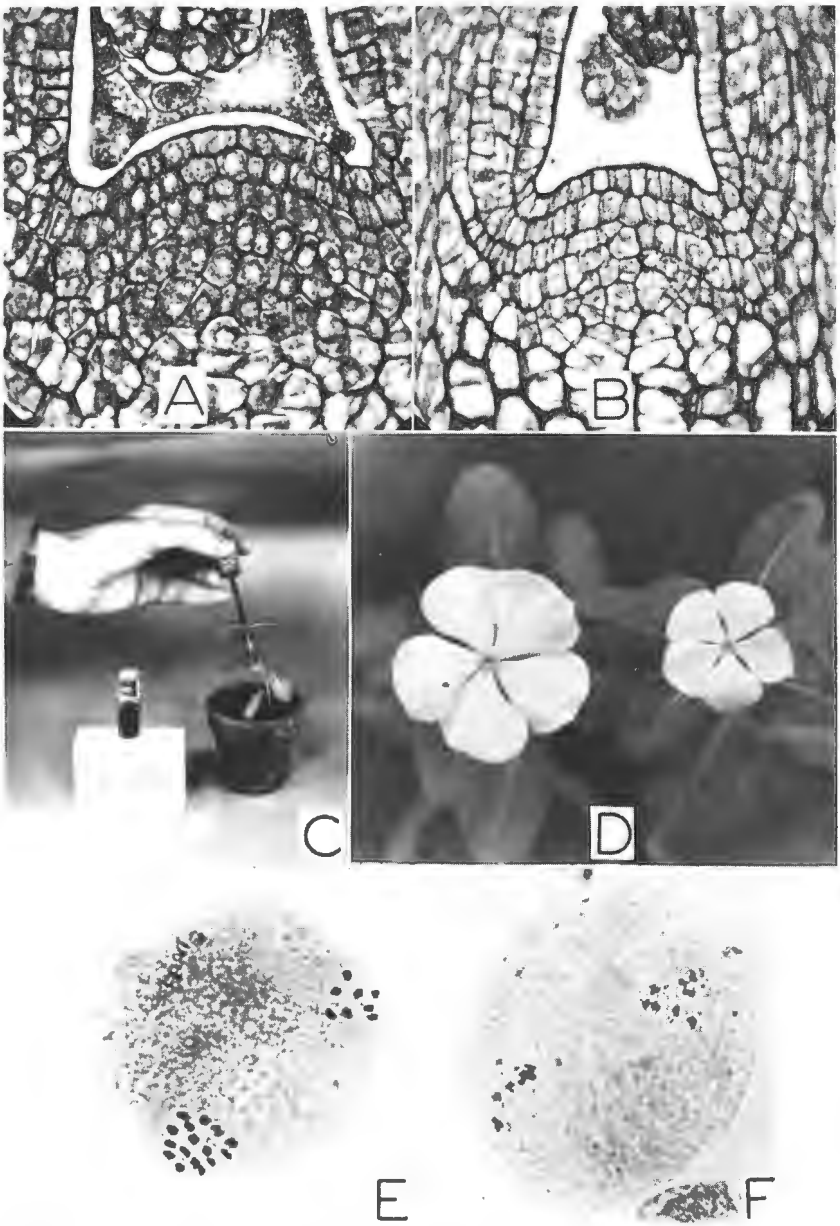


Fig. 14.1—A comparative study of **Vinca rosea** L. diploid and tetraploid strains. **A.** Shoot apex of tetraploid plants showing layers of cells, outermost is the first tunica or $T_1$, second layer $T_2$, third layer $C_1$, and deeper strata become $C_2$, etc. **B.** Shoot apex of diploid plant and foliar primordia. **C.** Brush method for treating yaung plants with colchicine. **D.** Size differences between the tetraploid and diploid flowers. Larger flower is tetraploid. **E.** Tetraploid pollen mother cell, n—16. **F.** Diploid pollen mother cell, n—8. (Contributions from the Botany Department, University of Oklahoma, Norman, Oklahoma. Adapted from Schnell)

parts and leaf. Since the cells of the first layer at the apex always divide anticlinally and not periclinally, all epidermal cells trace their origin back to the first layer as seen in the shoot apex. Accordingly, the second layer divides anticlinally, and tissues originating from the second layer will be independent in genetic make-up from the first, and in many cases from the third. If colchicine changes the cells of the first layer to tetraploidy while the second layer remains diploid, then the epidermal cells will be tetraploid and the pollen grains diploid, because the sporogenous tissues originate from the second layer. This condition is called a periclinal chimera. Various combinations can be had.

When geneticists realized that the treated plants might look like tetraploids yet reproduce as diploids, the significance of periclinal chimeras began to be truly appreciated.[7, 8] Moreover, developmental problems can be traced with closer attention to the origin of tissues, because specific periclinal chimeras should yield certain results in the mature organs.[42, 43, 44] If the pollen develops from the second layer, $T_2$, just beneath the epidermis, which is $T_1$, then diploidy and tetraploidy will be found in pollen and epidermis according to the changes in $T_1$ and $T_2$. That is to say, a tetraploid second layer, $T_2$, should produce tetraploid pollen mother cells while diploid guard cells originate from diploid $T_1$. The situation has been proved to be just that way. These are periclinal chimeras.

An important series in *Datura* was clearly described showing that the development of petals, sepals, pistil, ovules, and stamen could be traced back to specific layers of the apical meristem. Similar periclinal chimeras were found in the cranberry.[16] Cyto-histological changes were described in detail. One important conclusion was reached. Stem and lateral bud apices were seldom converted into total polyploidy. Therefore, semiwoody and woody plants propagated following treatment with colchicine, required special attention with care given to the nature of polyploidy induced.[16] Periclinal chimeras following treatment with colchicine have been reported many times since the first cases were reported for *Datura*.[42, 45]

By induced polyploidy, specific and discrete layers were demonstrated for *Datura stramonium* L.[42] The leaf and flower were traced back to the shoot apex. One important type useful in detecting origins was a diploid outer layer, an octoploid second layer, and a diploid third layer.[42] Any tissue that originated with an octoploid layer was unquestionably marked by the size of cells. Development of the carpel was traced in *Datura*.[42] The periclinal chimeras were used to discover specifically how the style, stigma, calyx, and corolla differentiated. In questions regarding axial or foliar origin for such parts as the stamen it can be stated more precisely how development takes place.

When numerous periclinal chimeras were demonstrated among well-known varieties of apples, interest was again intensified because the breeding behavior depended upon the specific chromosomal nature of a particular chimera.[15, 16] If the layer that produced pollen was diploid, triploid, or tetraploid, then entirely different results in hybridization could be expected. Periclinal tetraploid giant sports of McIntosh should be of great interest since tetraploids in subepidermal layers breed on the tetraploid level.[16] Some important varieties are triploid, many are diploid, while some sports are chimeras. Two naturally occurring chimeras in apples are: (1) the 2-4-2 type and (2) the 2-2-4.

The pomological curiosity known as "sweet and sour" from the Rhode Island Greening is meaningfully interpreted as a periclinal chimera. The sour portion originates from the outer layer and the third layer, whereas the sweet portion takes its origin from the second layer.[16]

Seven years after colchicine treatment, a McIntosh tree bore fruit that was giant-like, and similar to the diploid-tetraploid periclinal sport which occurs in nature. The induced type proved to be a periclinal chimera. By adventitious buds that originate from deeper layers, a complete tetraploid stock can be obtained. When crossed with diploids, this becomes breeding material for new triploid varieties. With better knowledge of periclinal chimeras, breeding in many fruit trees can be expected to advance.

Another kind of chimera is the sectorial chimera. As the name implies, sectors are either diploid or tetraploid. The changes occur in a mass of cells not limited to layers. This type was studied in *Datura*.[8] One branch becomes tetraploid and another diploid, depending on the origin of a specific branch.[7]

The wide distribution of periclinal chimeras in polyploids derived from colchicine shows that the change is not unusual. While our discussion is limited to only a few species, important work has been done with *Lilium*, *Solanum*, and many other plants. The principles as outlined with fruits and *Datura* are basic to all chimeras.

### 14.4: Sex Determination and Polyploidy

As was stated in the introduction to this chapter, polyploidy and special problems in botany did not arise suddenly when colchicine became known for its use in research. At this time, however, there was an immediate increase in papers dealing with such problems. A notable case was the relation between sex and polyploidy in plants.[55] One may erroneously conclude that new ideas were conceived as soon as colchicine was discovered. A proper perspective is needed here to evaluate properly the role played by an improved method such as colchicine proved to be. Whether the colchicine technique had

been developed then or not, a proof that dioecious races in plants could be established as polyploids would certainly have been reported when it was, in 1938.[55]

As early as 1925 the similarity in ploidy between animals and dioecious plants was observed.[53] Both cases were generally diploid. Among many plants polyploidy was a mode of species formation. These were not dioecious. Therefore, an explanation for the lack of polyploidy in animals and in dioecious plants seemed to be related to the diploid state. When a polyploid species of *Empetrum hermaphroditum* was found to be hermaphroditic, the fact was particularly interesting because there was a related diploid species, dioecious *Empetrum nigrum*.[55] Conflicting evidence accumulated when a dioecious tetraploid strain of *Vallisneria* was reported. Briefly this was the state of affairs when Westergaard decided to test the hypothesis by making tetraploids from diploid dioecious species of *Melandrium*. He began the project in spite of the fact that no well developed methods for making polyploids were available at that time. Colchicine had not been announced.[10, 55, 53]

In America, polyploidy and sex determination in plants were started because colchicine should quickly lead to the evidence needed to test the question raised by Muller about sex determination as limited to diploidy in animals and dioecious plants.[5] The projects in Denmark and America were started about the same time and first results from each came close together.[55] Yet there was no awareness that either was studying the same problem.

Soon other work began in Japan,[38, 34] and there were additional studies in America.[33] A large volume could be compiled from this problem after only a few years of investigation. Some excellent work was done and colchicine provided enough breeding material to demonstrate conclusively that sex determination was not limited to a diploid state when plants were under consideration. However, male and female plants are not strictly comparable to maleness and femaleness among animals. In plants there are three kinds, with respect to production of flowers: (1) plants producing staminate, or pollen-bearing, flowers, (2) some giving pistillate, or seed-producing, flowers, and (3) plants that have staminate and pistillate structures in the same flower. These are called male, female, and hermaphroditic, respectively.[55]

Adopting the sex-determining code used for animals, notably *Drosophila*, diploids are *XX* as females and *XY* for males; in addition there are other chromosomes called autosomes. A tetraploid female carries the chromosomes *XXXX* and male *XXYY* with a tetraploid set of autosomes designated *4A*. At once, it can be seen that another combination *XXXY* may exist at the tetraploid level. If further

crossing between tetraploids and diploids and between triploids and diploids were carried out, combinations could be extended to *XYY*, *XXXY*, *XXXYY*, *XXXXY*. Obviously, a great range may be produced. Everyone agrees that the *Y* chromosome is a determiner for maleness because the presence of this chromosome once or twice clearly impresses its influence on the plant. Only when four *X* chromosomes are opposing the one *Y* does the flower change to a hermaphrodite. This tendency begins to show slightly among the *XXXY* type. The *XY* and *XYY* are male without exception.[53]

The Danish[55] and American[53] polyploids differed with regard to the possible influence of autosomes and the role of the *X* chromosome as a female determiner. Some of the differences may be due to sources of diploid plants and some difference to method as well as interpretation. Two critical papers must be studied if one wishes to weigh the evidence: one by Warmke,[53] and another by Westergaard.[55]

Cytologically the *Y* chromosome can be distinguished from the smaller *X*. In turn, the *X* is larger than any autosomes. This feature is highly desirable because certain problems would be difficult to interpret otherwise. The hybrid generation between tetraploid *XXXX* and tetraploid *XXYY* throws 1 female to 12 males. The diploid sex ratios are 1:1. Looking at the chromosomes, it can be seen that most males are *XXXY* (89 per cent) and only a few *XXYY* (4 per cent). The association between *X-Y* and *Y-Y* is more frequent than between *X-Y* and *X-Y*. A high proportion of gametes were *XY* and the *XX* and *YY* classes were low. If a male with chromosomes *XXXY* was crossed with a female *XXXX*, the offspring showed 50-50 male:female ratios. Similar results were obtained with *Acnida tamariscina* (Nutt.) wood,[33] and for *Melandrium dioecum* var. *album* described above.[54]

In nature, the excess 4*n* males that are *XXXY* instead of *XXYY* would fertilize a large majority of the 4*n* females *XXXX;* hence, equal populations of males and females at the tetraploid level could be expected. From an evolutionary standpoint tetraploids differing on the basis of *X* and *Y* determining maleness and femaleness could be established much the same as a diploid species. A tetraploid race of *Rumex acetosa* has not been demonstrated as a stabilized dioecious type.[54]

Autotetraploid hemp gave an excess of females in the second generation following polyploidy.[34] This was a reversal over the diploid male-female proportions. Less cytological attention has been given to this species.

Polyploidy provides a method for deciding whether the male or female is heterogametic, that is, carrying the *XY*. A test was made for *Silene otites* since cytological methods did not give a solution in this case.[53] Polyploid plants would become *XXXX* and *XXYY*, but

the designation of male or female remains unknown. Crossing these tetraploids gives three types of offspring, *XXXX*, *XXXY*, and *XXYY*. About 5 males to 1 female are obtained. The female is tested by making triploids, mating tetraploids with diploids. A female *XXXX*, the $3n$ population crossed to male *XY*, should be 1:1, male, female. If the $3n$ population is 5 males to 1 female the constitution would be *XXYY*. The tests showed 1:1 ratios; thus females were homogametic as in *Melandrium*.

### 14.5: Aneuploids and Colchicine

Aneuploids can be created by colchicine in two ways. One procedure involves direct action on dividing cells in meristems.[4] The other method is indirect, following specific breeding procedures after polyploids have been made. Until colchicine was discovered, the first types were very rarely seen, particularly the diploid deficient plants, $2n - 1$. These were discussed on page 347. In this section the better-known, indirect method for developing aneuploids is discussed.

The scope has been expanded to more species because colchicine has stimulated the production of tetraploids. It is well known that tetraploids crossed with diploids create triploids. These in turn, when crossed back to diploids, become a rich source for off-type plants, those with extra chromosomes. Among the higher levels, pentaploids are excellent sources for aneuploids. Propagating autotetraploids regularly throws plants with somatic numbers deviating from the euploid value.

Distribution being unequal at meiosis, the chromosomes in the megaspore mother cell and the pollen mother cell cause the numerically different types. Sometimes transmission of extra types can be done through the seed parent only. In other cases the transmission of certain aneuploids is known only at high levels of polyploidy. If a particular morphology of the plant can be identified with aneuploidy, spontaneously occurring cases are usually high enough to create a large reservoir of extrachromosomal types.

Aneuploids among *Datura, Zea, Nicotiana, Triticum,* and other genera have been studied extensively and have been used for specific genetical tests before colchicine methods came into prominence. In other instances, such as *Gossypium*,[3, 11] their isolation in large numbers began when this ready method for producing polyploids was discovered.

*14.5–1: Trisomics and tetrasomics.* In 1915, A. F. Blakeslee found a mutant in the cultures of *Datura stramonium*. This was called the "Globe mutant" because this plant had a globose capsule distinct from the usual patterns. Five years later, in 1920, John Belling

demonstrated cytological evidence that this plant and others found between 1915 and 1920 each contained a single extra chromosome. In 1938, a summary covering 60,000 field-grown offspring from types with extra chromosomes was published.[6] The term *trisomic,* as the extra chromosomal plant was called, is used in cytogenetics.

With the use of colchicine in polyploidy and in *Beta* there arose an opportunity to study the effect of chromosomal variation in sugar beets.[30] It is one of the most intensively studied species as well as one of great practical importance in many countries. The large-scale production of tetraploids in 1938 with subsequent triploids opened opportunity to study variation in regard to chromosomal numbers. Since triploidy was discussed in the chapter on autoploidy, that will not be repeated. Here the influence of separate chromosomes, the trisomics, are of special consideration.[30]

Progenies from triploids intercrossed, and backcrossed to diploids, included plants with chromosomal numbers from diploid to tetraploid and beyond. One or more plants ranged from 18 to 36 chromosomes.[30] Between 37 and 45 several classes were missing. This material arose from colchicine-treated seed of the Hilleshog strain at Svalof, Sweden. When the seed parent was a triploid and the pollen parent diploid, all numbers from $2x$ to $3x$ were recovered. A reciprocal cross yielded an excess of diploids (77 per cent) with classes from 21 to 25 missing. The transmission difference between seed and parent confirms what had been learned long ago. Extensive pollen tube studies by J. T. Buchholz demonstrated the effect of extra chromosomes in *Datura* upon the male gametophyte.

Effects of different chromosomal classes upon a whole series of morphological and physiological characters in sugar beet were compared. Since this study permitted analysis of the entire population, certain advantages were presented that had never been possible before this time. Every chromosomal class from 18 to 36, inclusive, was analyzed as follows: (1) field estimation, (2) weight of tips and roots, (3) refractometer determinations, and (4) leaf development. The trisomics were distinct in plant characteristics, and the particular chromosome stamped its influence on growth habit. An interesting problem that requires more attention is the possible correlation between vigor increase and decrease in the size of the extra chromosome. This point becomes important when transfer of characteristics by single chromosomes is attempted. In addition to single trisomics, two plants with 20 chromosomes were studied. Plants beyond the 36 chromosomes, including a 42-chromosome plant, had good vigor. Finally the optimal numbers as would be predicted have three modes; these are diploid, triploid, and tetraploid. Maximum viability occurs at the euploid number.[30]

Five different chromosomes from *Nicotiana langsdorffii*, a small flowered species, was studied as trisomic in relation to corolla size. The background into which the extra chromosome was introduced was the hybrid between *N. langsdorffii* and *N. sanderaca*, a long-flowered species.[48] Since each trisomic could be detected by plant appearance the influence upon particular structures could be ana-

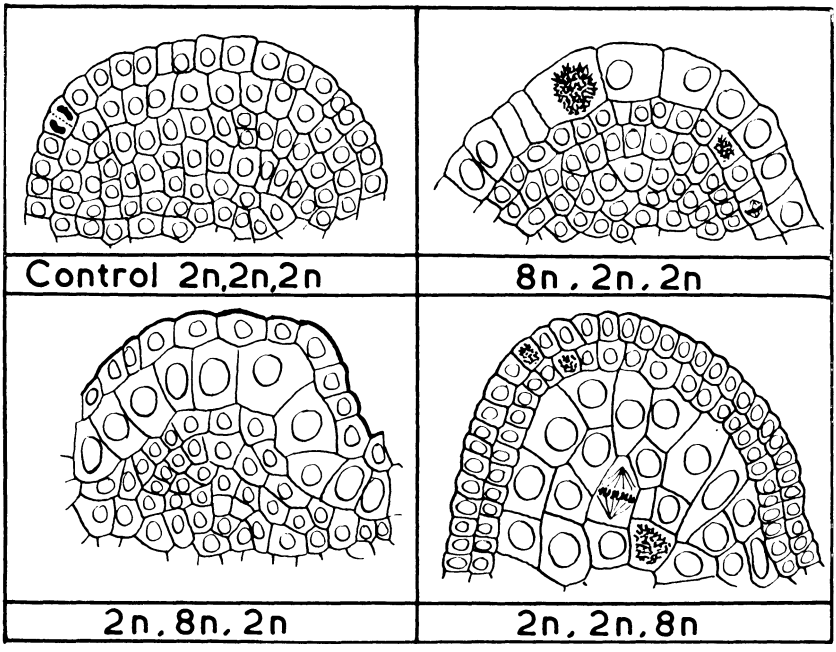


Fig. 14.2—Diagrams of longitudinal sections through the shoot apex of diploid **Datura stramonium** L. and three layers of periclinal chimeras. **Upper left,** diploid layers of tunica and corpus. **Upper Right,** octoploid tunica and diploid layers beneath. **Lower left,** first tunica diploid, second tunica octoploid, corpus diploid. **Lower right,** tunica diploid and corpus octoploid. (After Blakeslee and Satina)

lyzed. Three of the five chromosomes, when in trisomics, reduced the corolla in all regions, but two chromosomes decreased one region and increased another. This method was applied to find the relation between whole chromosomal additions and size effects. The conclusion was reached that size is determined by genes according to a geometric proportion. Eventually, size in *Nicotiana* flowers can be resolved as a "cumulative geometric effect."[48]

Hexaploids combining two species of *Gossypium* crossed back to *G. hirsutum* lead to aneuploids with one or two chromosomes from the diploid species introduced in the hexaploid. The characters influenced are: leaf, floral parts, size and shape of bolls, as well as fiber

and seed coat. Cytological study of these trisomics is valuable for determining the nature of chromosomal differentiation among specific chromosomes.[11]

Some fertile, partially stable plants can be derived by selfing inter-species trisomics instead of the tetraploid number or the extra chromosome; morphologically distinguishable 54-chromosome lines were produced. The interest in these types lies in their constitution because the extra pair may be from an Asiatic-American wild or an African species. This pair is added to the naturally occurring *G. hirsutum*, a tetraploid 52-chromosome plant.[11]

Another type, the *intra-species trisomics*, arises from polyploids of *G. hirsutum*. By selfing and appropriate crossing between various trisomics in this class, both double trisomics and tetrasomics were developed.

There are then two types of tetrasomics identifiable by the extra pair, the intra-species tetrasomic and inter-species tetrasomic. As the word suggests, the latter pair is derived from strains from another species, whereas the intraspecific tetrasomics are limited to one species.[11] Morphologically both types may be distinguishable from the species. A remarkable fertility is retained when a pair comes from another species, but the intraspecific tetrasomics are almost completely sterile. A great many cytological problems can be solved with these types. Trisomics and tetrasomics have been obtained in *N. sylvestrus*. Among the off-type plants from a progeny of monoploid pollinated by diploid, trisomics were derived in wheat. Further selfing yielded tetrasomics. These added chromosomal types are not easily detected in hexaploid wheat. Some homozygous speltoid wheat proved to be 44-chromosomal plants. Tetrasomics and trisomics may have been involved in the dwarf and subcompactoid types.[31]

*14.5—2: Nullisomics and monosomics.* Chromosomes lost in diploid plants do not survive. This was reviewed in an earlier section. Tetraploids in *Datura* also lacking a chromosome or two failed to set seed. Additions in diploids have been propagated extensively, but these are often transmitted only through seed parents.

At the polyploid level, missing chromosomes are tolerated.[27] For that reason some important work can be done with two general types: (1) monosomics, those plants lacking one chromosome, and (2) nullisomics in which a pair is missing.[51] The latter are well known among hexaploid wheat.[46] In *Gossypium* and *Nicotiana* a success similar to that for hexaploid wheat has not been achieved with nullisomics.[12]

Monosomic plants have been found in *Gossypium* spontaneously, through nondisjunction in trisomics, and after intergeneric pollination.[11] Since the transmission of haplo-deficient gametes fails in *Gossypium*, the further utilization of monosomics is stopped. In contrast

to this situation, monosomic analysis developed for *Nicotiana* has proved most useful in many genetic tests, notably in establishing linkage groups; surveying amphidiploids for specific genetic characters.[12] The technique applied to *Nicotiana* suggests that other groups might profit from these methods.[23] There are limitations to this method among such a group as *Gossypium*, where polyploids are common; yet the use of monosomics is limited. No nullisomics are reported for *Gossypium*.[11]

Quite another situation exists in hexaploid *Triticum aestivum* L., where nullisomics and monosomics can be applied to genetic problems.[51] As we mentioned for trisomics, the number of different types with one whole chromosome extra should equal the haploid number. For *Datura*, 12 primary trisomic types exist. In *Nicotiana* the total monosomics possible is 24. Accordingly, 21 nullisomics would be expected or equal to the 21 pairs representing hexaploid wheat.[46]

For each pair missing, the 20-chromosome plant has specific characteristics. Nullisomics may be numbered from I to XXI.[46] None is completely sterile, and certain are fertile in both male and female. Some are female-fertile only, others male-fertile only. Some nullisomics pollinated by normal plants give more monosomes of a particular type, as well as trisomes. The incidence is more than a random occurrence. For example, nullisomic III produced more monosomic IV and XV than other types of monosomes.

Particular tetrasomics may cancel the effects of certain nullisomics. Such compensating cases are known for wheat and oats. For example, tetrasomic II compensates for nullisomic XX so that the plant is very nearly normal even as the male gametophyte.[46] There does not seem to be a competitive advantage between pollen-deficient for chromosome XX and duplicated for II. Common properties in the segments of these chromosomes would appear to be a cause for the compensation. There seems to be no pairing between tetrasome II and nullisome XX. These are, in very brief sketch, problems related to polyploidy.

Seven chromosomal pairs corresponding to the *D genome* in hexaploid wheat are dwarf nullisomics and differ from each other according to the specific pair missing. These nullisomics were derived from among offspring of *Triticum polomicum*, genomes *AABB*, $\times$ *T. spelta, AABBDD*. These 7 nullisomics are lettered *a, b, c, d, e, f, g*, respectively. Twenty-one nullisomics from a Chinese wheat (*T. aestivum* L.) should throw light on the *D* genome by hybridizing the dwarf nullisomics and those from *T. aestivum*, which had a different origin.[31]

Success has been achieved in transferring mosaic disease resistance from one species to another in *Nicotiana*. The commerical tobacco re-

ceived a chromosomal pair from *N. glutinosa,* which contributed the necrotic factor for resistance. Alien additional races included a pair from one species and 24 pairs from *N. tabacum.* By another series of crosses, alien substitution races were formed, whereby a pair of chromosomes were substituted in the *N. tabacum* genome.[23] Other species carry factors that can be traced by successive crosses into the interspecific hybrid, then by a backcrossing procedure through a number of generations. The monosomic method of analysis has been worked out with good success in *Nicotiana.*[12]

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