

The Autoploids

13.1: Autotetraploids

Oenothera lamarckiana, var. *gigas*, discovered by Hugo de Vries at the beginning of the twentieth century, proved to have twice the number of chromosomes found in a related species. After colchicine became known, this classic polyploid was repeated.²⁰⁷ Plants with the doubled number of chromosomes are not considered mutants, even though originally the concept of mutation advanced by de Vries was in part taken from his experiences with *Oenothera*. Increasing the number of chromosomes increases the number of genes, not the kind. No one would consider as mutations the production of diploids from monoploids,³¹ or of triploids from hybrids between tetraploids and diploids. Colchicine is not a mutagenic agent in any sense, either for production of chromosomal changes or in its capacity as a polyploidizing agent.³⁴

Without exception, the autoploids produce fewer seed than the diploid from which they originated by doubling. Great variations in fertility are found from species to species, from almost total sterility to values as high as 75 per cent.²⁰³ In subsequent generations the fertility level can be raised. Among tetraploid *Melilotus alba* two groups of tetraploids have been isolated, high-fertility and low-fertility lines.⁹¹

Many comparisons have been made between diploids and the related tetraploids, on a physiological, morphological, chemical, anatomical, ecological, as well as cytogenetic basis. The differences are well known, and the original *gigas* features have been demonstrated over and over.

Certain problems relating to chromosomal mechanisms and fertility have not yet been solved. Less and less agreement is found on the causes for lowered fertility in the autotetraploids. Autotetraploids from homozygous lines of maize are less fertile than the correspond-

ing types from heterozygous diploids.¹⁷¹ Comparative studies in *Antirrhinum* showed that between intravarietal and intervarietal tetraploids the problem of fertility involves something more complex than a mere analysis of meiotic disturbances created in the tetraploids.²⁰¹

The ecological requirements of autoploids are not as distinctive from the diploids as are these requirements in amphiploids and their parental diploids.³⁴ Hybridization does not activate processes in autopolyploidy, and evolution at the tetraploid level must occur through gene and chromosomal changes which are undoubtedly very slow.

From a practical standpoint, the lowered fertility at once placed the tetraploid at a yield disadvantage. But these facts were well known before colchicine was discovered. The problem in using tetraploids becomes one of balancing the advantages against the disadvantages, and then measuring the net gain, in comparison with the accepted competing diploid varieties. The use of polyploidy is not a quick way to develop new and improved varieties. Some projects were undertaken with high hopes that revolutionary methods were at hand. By now most of those concepts have been revised. For some, polyploidy has been totally dropped as a method for improving varieties. These are instances where the techniques should never have been started; in others, the programs are stopping short of probable success. Revised programs using polyploidy are in progress in many laboratories throughout the world.

13.1-1: The cereals and polyploidy. In the autumn of 1951, large quantities of seed of autotetraploid steel rye were distributed to farmers in Sweden.¹³² The first tetraploid rye was made before colchicine was discovered and it proved to be inferior. Therefore, one might suspect other polyploids in rye to be poor. Several more polyploid varieties induced by colchicine have also proved inferior to the best diploid varieties. There were variations in the different tetraploids as well as variation among plants. Finally a superior tetraploid was derived from a diploid variety of steel rye, and this formed the beginning of this valuable series.¹³² A report on the cytogenetics and practical value of tetraploid rye is a good guide for steps necessary to develop tetraploid varieties.

Testing the performance of tetraploid rye and diploid varieties was difficult because plots could not be planted side by side. The diploid pollen falling on tetraploid flowers greatly reduced the seed yield of the tetraploid. Therefore, special tests had to be worked out before a demonstration of practical value for the tetraploid rye was possible.

Like all autotetraploids, the cell size was larger than that of the diploid. Pollen measurements were a reliable index for tetraploidy, but even less complex for practical selection was the size of seed,

which was larger among tetraploids. When large populations were studied, the diploid and tetraploid spikes could be separated by using the size of seeds for comparison. This was quite as safe as making pollen measurements, so the need for counting chromosomes in the preliminary stages of sorting was not required.¹³ Such rules can be adopted for other projects.

In regard to vegetative and floral characters, the tetraploids were taller and of stiffer straws; the degree of tillering was lower; and the number of flowers was reduced. But kernel size and weight exceeded that of the diploid. However, the hectoliter weight values were lower. Tetraploid steel rye had good sprouting ability and was able to stand the winter conditions as well as diploid rye. There were no marked differences in maturity values between the two types. The baking quality of the flour of the tetraploids was superior to the diploid in the preparation of both the soft and the hard breads.⁴

Morphologically, the tetraploid rye, like most autopolyploids, showed the following differences from the diploid: (1) stems were thicker and stouter; (2) tetraploids were taller; (3) leaves were larger; (4) leaves were thicker; (5) leaves were somewhat shorter and broader; (6) leaves were greener; (7) floral parts were larger; and (8) seeds were larger.¹³²

From a practical standpoint, the advantages gained by tetraploid steel rye over the diploid arose from a favorable balance of two positive properties as against the four more or less negative characteristics. The lower seed setting (20–25 per cent), reduced tillering, lower number of flowers per spike, and tendency to shed basal spikelets, were counterbalanced by the superior baking quality of the flour and the improved sprouting ability of the seed.¹³²

Artificially produced tetraploids in rice have been made with a number of important varieties.¹⁰³ The tetraploids were distinctly larger-grained, heavier-awned, and more robust generally. While the grains were heavier, a reduced fertility counterbalances the gain in weight per grain. Here again tetraploids manifest the usual disadvantage. These raw tetraploids were without immediate practical use for the reasons already well known. Moreover, there was much doubt that by further selection the fertility could be raised high enough to overcome the yield disadvantage from a reduced fertility.

Another approach to polyploidy as a means for improving rice was made. The F_1 hybrids *Oryza sativa* var. *indica* \times *O. sativa* var. *japonica* are very sterile in some combinations. This sterility has blocked the possible utilization of a hybrid between the subspecies. There is no apparent meiotic irregularity in the hybrid, and the causes of sterility remain unknown. Autotetraploids seldom exceeded

60 per cent fertility, while in the parental diploid fertility was over 90 per cent. Yet the hybrid between the subspecies *japonica* and *indica* may even drop to 11 per cent when fertility is measured by seed formation. Sterile F_1 's, if doubled, immediately raised the seed formation higher than autotetraploids.³⁶ As the fertility decreased in a given F_1 hybrid, the fertility increased in the corresponding tetraploid. That is, the more sterile the diploid F_1 hybrid, the higher was its restoration of seed fertility after doubling.³⁶ Pollen sterility approximated the same rules. Thus the disadvantage met by strict autotetraploidy seems to be overcome in this type of program. Some real obstacles may yet be encountered in trying to stabilize the polyploid that combines *japonica* and *indica* genomes. Further segregation must be studied.

No quick results can be expected in spite of the apparent solution to the fertility problem, for the tetraploids from hybrids are, like all tetraploids, unselected. Judging from the high multivalent formation, segregating progenies in F_2 and later generations can be expected. This fact may offer exceptional plant breeding opportunities along with serious obstacles. Obviously, these plants and such methods will receive attention in the future as another approach toward plant improvement in rice.

An extensive literature is devoted to autotetraploid barley.²⁰⁰ Some spontaneous $4n$ races have been isolated. Also, colchicine has been used by several investigators. Morphological characters that change with polyploidy are well catalogued along with several excellent physiological studies. The progress has been summarized in a comprehensive review, and little more need be added. The practical uses for barley have not come up to those of autotetraploid rye.

Autotetraploid maize has been followed over a long period, since the earliest strains were made by heat treatment, before colchicine methods were available. Fertility differences cannot be correlated entirely with chromosomal processes at meiosis. The slower growth and reduced fertility are disadvantages of the tetraploid. The doubling of monoloids to autodiploids will be developed in another section.

Other cereals of economic importance, being natural polyploids, require other approaches. The autopoloids are inferior to diploids and provide genetic materials only.

13.1—2: *Forage, range, and pasture species.* Raw polyploids in some species of *Trifolium* showed an immediate advantage over the diploid in forage production.¹¹³ The data were obtained from limited scale testing. When the tetraploids were distributed for larger scale trials, the difficulties not encountered with small tests then appeared.³

After revising the methods for making tetraploids and choosing much larger samples, 50 commercial varieties of red clover, new tetraploids superior to the first, were developed.

In Scandinavian countries notable progress has been made with red clover, *T. pratense*. Twenty-eight chromosomes does not appear to exceed the optimal number. The yield of forage is also independent of seed production. The seed setting becomes important for propagation purposes but not yield of forage. At least five major tetraploid varieties have been tested over several areas in Denmark, Norway, and Sweden. The results are encouraging as a method for improving red clover by polyploidy.^{113, 63, 92, 220} It is of interest that the new tetraploids in red clover do not necessarily come from the best diploid strains. Only by testing the tetraploids can their true value be judged.

In addition to gigas features valued for forage production, the earlier and more rapid growth in the second year was better than in diploids. Undoubtedly, the tendency toward a perennial habit in polyploids would seem to be correlated with this trait. Susceptibility to insects and diseases are a weakness in most strains, diploids as well as tetraploids, but there were some red clover tetraploids with excellent insect and disease resistance. One red clover strain, Sv. 054, from a diploid variety Merkur had good yielding capacity and resistance to the nematode, clover eel.

Diploid alsike clover, *T. hybridum*, made tetraploid, showed promise at once, giving consistent increases in forage from 15 to 25 per cent. For overwintering capacity the alsike clover was good from the start.²²⁰ Continued successful performance stimulated a change to breeding on the tetraploid level. Without doubt, these two tetraploid clovers have made satisfactory performance.

A third species, *T. repens* (white clover), was not successful, but as this is a natural tetraploid, 32 chromosomes, further increases presumably took the number to 64, a number above the optimum for the species. We must conclude that one cannot draw a general rule for all clover breeding (cf. Chapter 11, Ref. No. 4).

The tetraploid *Melilotus* suffered from a reduced fertility and was not as promising for practical purposes, although there were enough differences in fertility among eight plants of tetraploids to make progress in selecting toward higher fertility.⁹¹ Crosses and selections demonstrated that higher levels of self-fertility could be obtained. If interspecific hybridization could be effected, the combined germplasm would open another avenue for analysis.

Polyploidy has been obtained in *Medicago sativa*, *M. media*, *M. lupulina*, and *M. denticulata*.²³⁴ Vigorous strains appeared among these polyploids; however, the usual reductions in seed setting were

met. Since there are diploids as well as natural tetraploids within the group, some hybridization would appear possible. The crossing of autotetraploids with natural tetraploids offers a method to be tried.¹⁴³

Phleum pratense was made up in chromosomal series, ranging from diploid to twelve-ploid.¹¹³ Analyses for vigor, forage production, and quality were done to check the optimum number, below or above which poorer performance was noticed. Progenies with 56 to 64 chromosomes were more vigorous than the 42-chromosomal plants or the polyploids with 84 chromosomes. This principle of optimum numbers must be recognized in polyploidy breeding. Hexaploid *Phleum nodosum* was made by first doubling the chromosomes with diploid *P. nodosum*.¹⁵² The tetraploid was treated again and a hexaploid was isolated. Of special interest is the close correspondence between the natural species, *P. pratense* L., and the hexaploid, *P. nodosum*.

Lolium perenne in the tetraploid state was compared to the diploids.¹³⁵ Morphological and physiological studies brought to attention characters such as winter injury, sugar content, dry matter, moisture, leaf structure, tillering, and flowers. The autotetraploids of seven species of grasses were compared in regard to both morphological and cytological details. No specific advantages were demonstrated for the tetraploids.

Autotetraploid Sudan grass, *Sorghum vulgare* var. *sudanense*, and Johnson grass, *S. halopense*, were hybridized to make a pasture species.²⁹ Autotetraploid Sudan grass incorporated better forage characters into the hybrid. One observation confirmed that the autotetraploid would hybridize while the diploid Sudan grass always failed. Later generations followed for this hybrid segregated for the dry and juicy stalk quality. The segregations were closer to 35:1 than 20.8:1, meaning that random chromosome segregation had occurred.²⁹ These polyploids showed a tremendous possibility for selection.

13.1-3: *Polyploidy in fruit, vegetable, flower, and forest species.* Polyploidy and fruit improvement in the United States have been summarized in this way. The problem is like that of a "builder surveying the possibilities of his materials and the usefulness of his tools." Materials are enormous and tools are now available. Colchicine is one of those important tools, while the materials include an abundance of plants in nature and under cultivation. "The only limits are his blueprint, his time, and his industry."³⁹

The diploid, woodland strawberry, *Fragaria vesca*, $2n = 14$, is found in many parts of the northern hemisphere. Cultivated varieties are octoploids, $8n = 56$. Autotetraploids from *F. vesca*, $4n = 28$, were made and crossed with 56-chromosome cultivated strains. Such hybrids were 42-chromosome hexaploids. These were crossed back to

cultivated types and provided material for selection.¹⁹⁰ Further search for natural species useful in polyploidy is underway. Disease resistance, flavor, quality, and size have been incorporated into hexaploids. There were reportedly 24 breeding projects in the U.S.A. engaged in various aspects of strawberry work. There are important cytogenetical strains in polyploid series at hand in the Botany Department at the University of Manchester, England.⁷³

Including wild and cultivated varieties, chromosomal series from $2n = 14$ to $12n = 84$ exist among the blackberries and raspberries. Perhaps no other fruit can be correlated any more directly to polyploidy than this one. The Nessberry, Logan, Boysen, along with hundreds of forms of polyploid blackberries are in existence. Since there are polyploids at hand, artificial doubling is not so necessary. Where faster progress may be required, or the changing of sterile hybrids to fertile ones, colchicine serves as a useful tool.³⁹

Many cultivated cranberries are diploid, and in nature, tetraploid as well as diploid species exist.^{42, 43} Some sterile hexaploids have been reported. By doubling the number of the cultivated diploid, a parental stock was made for crossing with the wild tetraploid. Selections from all the important cultivated diploid varieties were doubled. These types were selfed and hybridized. Such types have been grown on large scale since their origin, and raw polyploids are being converted into genotypically balanced types.

Perhaps polyploidy as a direct mode for improvement in grapes has advanced as far as any fruit crop of the United States. Here naturally occurring sports, often chimeras, proved to be tetraploid. They occurred in sufficient abundance, so that artificial doubling by colchicine has not been necessary. Giant fruited sports from the *vinifera* and bunch grapes are tetraploid.¹⁵⁵ These studies have progressed to a stage where newly named tetraploid varieties now combine important characters and are distributed as improved types.

Named tetraploid varieties of summer radish were released in Japan and tested widely enough to demonstrate a superiority for the new polyploid. In vigor and growth the tetraploid exceeded the diploid. Outstanding resistance to the common club root disease was obtained with the tetraploid. The usual *gigas* features accompany these autotetraploid radishes.¹⁴⁴

Polyploidy in water cress increased the succulence of leaves, which feature made the tetraploid strains more desirable for salads.⁸¹ Increased content of vitamin C in the water cress, which is expected in tetraploids, was an advantage over diploids. One disadvantage was the slower-growing characters of tetraploids. Like the autotetraploid rye, apparently a balance between the positive characters against the negative ones is needed. When an immediate superiority in favor

of tetraploids, such as leaf size, succulence, and vitamin content increase can be demonstrated, the promise for future polyploidy breeding offers some hope. Without some initial advantage or promise, the use of polyploidy must be questioned for practical purposes.

Direct autotetraploidy in tomatoes has not brought improvements. There seem to be hybridization possibilities.²⁴ Similarly, within the large group of *Solanum*, an interspecific hybridization is probably the most useful approach.²⁰⁹ *S. tuberosum*, the commonly cultivated species, is already polyploid; doubling is therefore of no value. *S. antipoviczii* \times *S. chacoense* amphiploid was fertile with *S. tuberosum*. By this procedure the disease resistance to phytophthora from one species, *S. antipoviczii*, should be transferable into a polyploid hybrid.²¹⁸ The advantages gained from such work can be maintained because vegetative propagation fixed the features once obtained.

The quality of tetraploid muskmelons, *Cucumis melo* L., was definitely superior to the comparable diploid variety.¹⁴ Enough seed can be produced to propagate the tetraploid adequately. These polyploids were made in several laboratories; each reported improvements. In one instance, taste tests were conducted in such a way that identity of ploidy was not revealed. Without exception, the choice fell to the tetraploid. Since ten different varieties were made tetraploid, a larger number of them were used in comparison with the polyploid and diploid.

A new potential economic species of *Cucurbita* was developed by doubling the chromosomes of a hybrid between *C. maxima* and *C. moschata*. One species, *C. moschata*, carried insect resistance to the hybrid while fruit characters were contributed by the other parent. These characters were not entirely stable in the hybrid, but showed more stability in the polyploid. Fruits matured earlier in the amphiploid than in either parent. In the first generation of the amphiploid there was little or no segregation. Later, up to the fifth generation, there appeared segregation for fruit color, shape, and size. Evidently some intergenomal pairing occurred, and occasional bivalents could be observed during meiosis of the diploid interspecific hybrid. A variant that resembled another species, *C. pepo*, appeared. This type was completely sterile to either the $2n$ or $4n$ lines. Since the same variant has reappeared, considerable theoretical interest becomes attached to this segregate. Large-scale tests in several locations showed that a new potential economic species of *Cucurbita* has been made (cf. Chapter 12).

The gigas characters accompanying induced polyploidy became attached to colchicine as soon as the effectiveness of this method was announced. Probably the first plantsmen to give serious attention to colchicine were those interested in developing ornamentals. The rea-

sons for this appeal of larger flowers are easily understood. One hundred and nine varieties chosen by iris fanciers from a total of 12 best selections were studied for chromosome numbers. Not one was diploid, but 108 were tetraploid, and one was triploid. Practically all these were developed and selected without studying chromosomes, but in this case the potential of polyploids was forcefully demonstrated.⁵⁴

It is no surprise to find many persons attracted to the possibilities to be gained from colchicine. Larger flowers were anticipated.

Among the first colchicine-induced tetraploids to be distributed were snapdragon, phlox⁵², and marigold. Work with carnation²⁰⁶, poinsettia²⁰⁶, day lilies²¹⁹, and lilies⁵⁴ has yielded tetraploids. There are numerous projects under way with many ornamentals, annuals, perennials, and shrubs. Improved flower size, darker and more compact plants, with greater drought resistance were obtained with tetraploid *Vinca rosea* L.¹⁸⁷ Also the flowering period was extended longer than in the diploid. While seed production was reduced, this disadvantage was balanced with other positive characters in the tetraploid.

13.1-4: *Plants yielding special products of economic importance: fibers, oils, latex, drugs, beverages.* Autotetraploids increased the size of seed, fruit, leaf, stem, and root, and larger plant organs should yield more substances of economic importance.²³⁶ Oil-bearing seeds such as sesame, *Brassica*, and flax, all have lower seed production as tetraploids. Flax is a notable case where the fertility drops extremely low. Rubber increase in *Koh saghyz* and *Hevea* are objectives. Fiber improvements in *Hibiscus*, cotton, flax, jute, and hemp have been sought via polyploidy. Anabesine in polyploid *Nicotiana* increased with polyploidy.

13.2: Triploidy

Hybrids from a tetraploid seed parent crossed with a diploid pollinator are triploid. As such these are not stable, and both male and female gametes are sterile from unbalanced chromosomal distributions. The vegetative vigor is not lowered, in fact many triploids are extremely vigorous. Among the good varieties of apples, triploids are common. In nature some triploid species are widely distributed. *Polygonatum multiflorum* is an example of a triploid having a range from the northwestern Himalayas throughout Europe.

The two kinds of triploids are the autotriploid and allotriploid. The former arises from an autotetraploid crossed back to the parental diploid, whereas the allotriploids involve two species. In these cases bivalents and univalents are found at meiosis. Triploids offer the opportunity for increasing the frequency of aneuploids since the triploid female gametes are viable with one or two chromosomes above

and below the haploid number. Another common practice is doubling the triploid to make hexaploids. Such a bridge is regularly followed in *Gossypium*, where the hybrid between American tetraploid and a species becomes a sterile triploid.

Certain advantages may be gained from triploids that are not possible otherwise. If the optimum chromosomal number is closer to triploid than tetraploid, production may be increased over either diploid or tetraploid. If ripened seeds can be eliminated or reduced, as in the triploid watermelon, a new type fruit is obtained. These features in triploids are limited but seem important.

Finally triploidy raises problems of seed production: an extra propagation of parental stocks to preserve the two types, as well as a specific hybridization to produce the seed for each generation. Success may depend upon solving these problems. Triploid seeds do not germinate as well as those of other polyploids. Furthermore, the cross between tetraploids and diploids cannot be readily made for all autoploids.

13.2-1: *Triploids in watermelons*. Reasoning from the fact that seedless fruits in nature are due to certain reproductive failures, the idea was conceived that seedless watermelons would result if triploids were made. The female sterility notable among triploids would lead to this achievement. Such work was initiated in Japan in 1939. Ten years later the first triploid watermelon fruits appeared on the market in Japan.^{97, 100, 101} This may be regarded by practical breeders as a very short time for the production of a new variety. Triploid watermelons were a new concept involving hybridization and polyploidy breeding procedures.

The tetraploid parents are produced by colchicine applied at the seedling stage. These plants have 44 chromosomes and are easily distinguished from the diploid by seed size, pollen size increase, and other characteristics. After the tetraploids are produced, these varieties become the seed parent with the diploids as pollinators to make the triploid.^{97, 100, 235}

Seeds obtained from a tetraploid fruit and pollinated by the diploid are triploid. Upon planting such triploid seed, fruits without seeds may be had. Early in the season, and late, the ovules develop hard coats that resemble seeds. These are empty, but the term *seedless* becomes meaningless when fruits show these cores or empty seeds. Therefore, the term triploid is far more desirable. To avoid these difficulties, the first pistillate flowers are removed to eliminate the fruits with seed shells.⁹⁷

When triploid plants are growing, pollinations must be made by diploids because the pollen of triploids (flowers) is not sufficient to induce fruit development. Thus, interplanting diploids with trip-

loids causes fruit development among triploids. However, the sterility of the female precludes seed setting even though viable diploid pollen is present. This is the general scheme in producing triploid watermelons that under specific circumstances set seedless fruits.

The general procedure of formation of triploid fruits is set forth diagrammatically in Figure 13.1. Only crosses involving the female

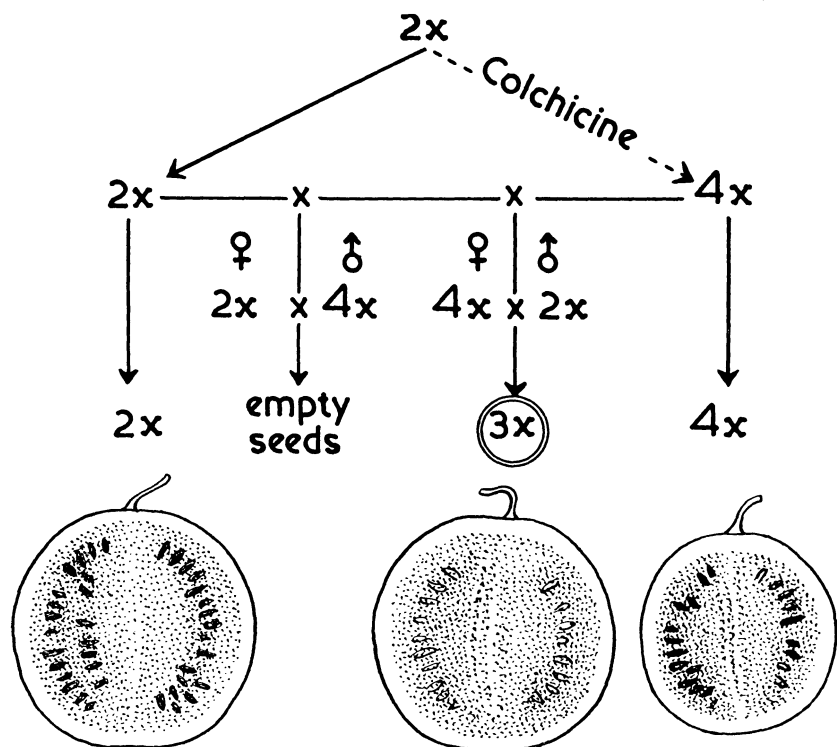


Fig. 13.1—Triploid watermelon. Propagation of triploid seed by crossing diploid and tetraploid lines. Use of colchicine to make tetraploid stocks. Fruits from diploid, triploid, and tetraploid stocks. (Adapted from Kihara)

as tetraploid and the male as diploid pollinator are successful. Reciprocal procedures do not succeed.

As in autotetraploids, the size of flowers increases in proportion to the increase in chromosome number. This relation holds for tetraploid pollen and stomata. Triploid pollen is variable in size and cannot be made to fit the proportional increase as chromosome numbers increase. Many grains are empty while others are full and may be huge.

The $3X$ seed is a tetraploid seed with triploid embryos obtained from a diploid pollination. The $3X$ seeds are slightly thinner, averag-

ing 1.7 mm. in thickness as compared with about 2.7 mm. for the 4X seeds. This feature is of practical value in sorting 3X and 4X seeds if the tetraploids are left to open pollination from tetraploid and diploid pollen in the same field. In Figure 13.2 the sizes of diploid and tetraploid seeds are contrasted.

If longitudinal sections are made of mature seed, the diploid, or 2X, seeds show a completely filled cavity, while the 3X and 4X seeds fill the space up to 82.5 and 90.1 per cent, respectively. Accordingly, a weaker germination is a characteristic of the 3X seeds. This becomes a point of considerable practical importance and must be overcome with proper culturing conditions. Such seed cannot be planted in the field with diploid and be expected to produce the same field stand for both varieties.

Genetic markers are helpful to distinguish triploid fruits from tetraploid and diploid. Dark-green, parallel striping is dominant over smooth color, therefore fruits pollinated by diploid with the stripe character show in the triploid if tetraploid fruits are non-striped. Tetraploid fruits may have this mark (Fig. 13.2).

Yielding capacity of triploid plants exceeds the diploid by almost twice. Variations appear depending upon the particular varietal combinations. The increase in number of fruits per unit area is particularly significant both as to number and weight.

Triploid fruits are seedless because chromosome distribution to gametes is irregular. Trivalent associations form among the 33 chromosomes. At reduction division, less than 1 per cent of the gametes obtain a complete set of 11 chromosomes necessary for a balanced gamete. Ninety-nine per cent have numbers ranging from 11 to 22 chromosomes. Sterility is induced, and pollination with viable pollen does not produce seed because of female sterility. When pollinations are prevented on triploids, fruits do not set.

Special cultivation procedures are necessary for triploid watermelons: soil should be sterilized, seed planted in beds kept at 30°C., and transplantation procedures carried out to insure a field stand of vigorous plants. Once the triploid is established, its growth exceeds that of the diploid and continues longer during the season. A ratio of 4 or 5 triploid plants to 1 diploid provides adequate pollen to set fruit on triploids; the latter become parthenocarpic.

A summarizing paper by Professor H. Kihara of the Kyoto University, Kyoto, Japan, on triploid watermelons, published in the Proceedings of the American Society for Horticultural Science,⁹⁷ was recognized as an outstanding contribution to horticultural science. Accordingly, this publication was chosen to receive the Leonard H. Vaughn Award in vegetable crops. The published works from Volumes 57 and 58 of the Proceedings were considered in the competition for this honor.

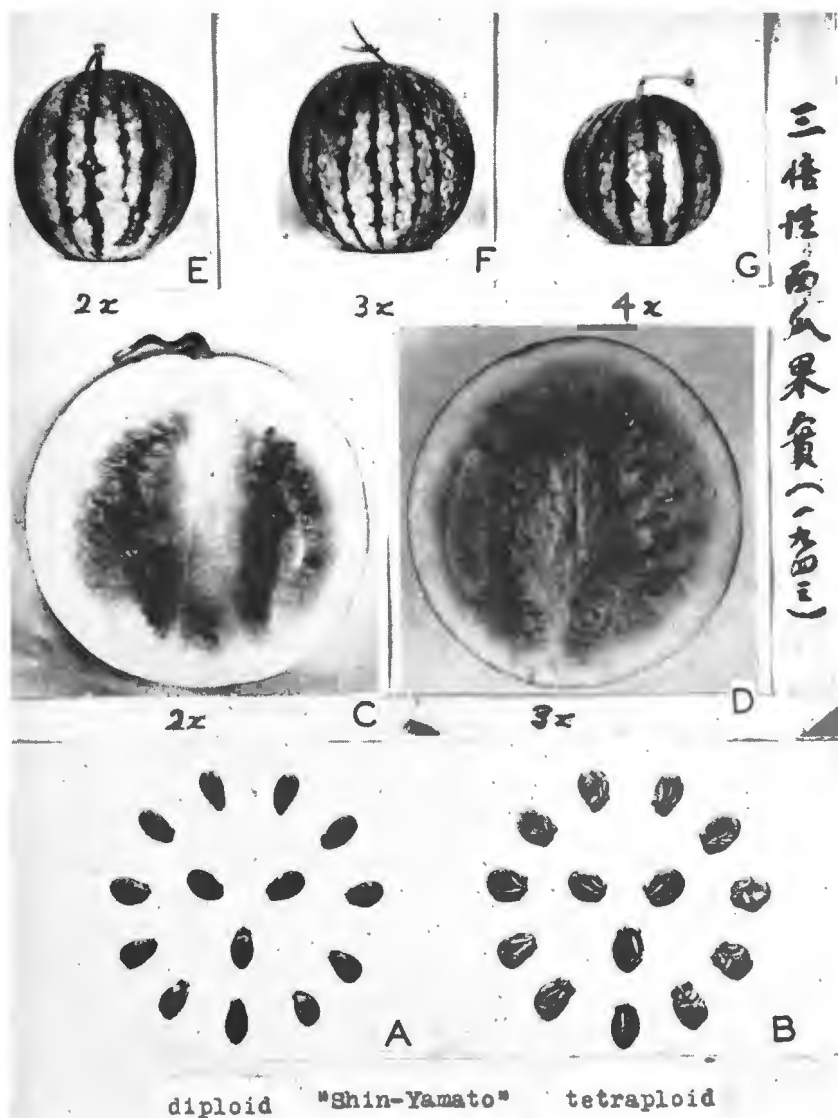


Fig. 13.2—Photographs of diploid, triploid, and tetraploid fruit and seed. (Photographs furnished by Professor H. Kihara, Kyoto, Japan)

In Japan, production of triploids as a method for improving watermelon production has been successfully explored. The opinions of American horticulturists on this subject vary with the experiences gained from testing the Japanese varieties. Success is reported in personal communications from Professor E. C. Stevenson, Purdue University, Lafayette, Indiana, and Professor W. S. Barham, North Carolina State College, Raleigh, N. C. Undoubtedly other unpublished reports in America and elsewhere concur in many of the general observations published by Kihara and his associates relative to yield advantages, disease resistance, and improved quality.

Seed production and wide-scale commercial growing will increase as better adapted varieties are made available. Some problems peculiar to cultivating triploids and to seed production need attention in the American system. If watermelons of better quality can be obtained, fruits produced without seeds, or almost so, and if triploid varieties are placed in the hands of commercial growers who can produce melons more profitably than by present methods, the problems of seed production and triploid cultivation will eventually be solved. The time required for this transition in America is difficult to calculate; however, the records of acceptance of hybridization in maize set a standard that might well obtain in watermelon seed production and commercial growing of this fruit.

The application of colchicine to the problems of watermelons represents a most specific and outstanding practical advantage gained from the use of this drug.

13.2-2: *Triploid sugar beets.* Early in the colchicine era polyploidy breeding was directed at the improvement of sugar beets. Raw tetraploids did not prove to be as good as the parental diploids. This was to be expected for reasons outlined in the section on principles of polyploidy breeding.^{8, 63, 113, 114, 122, 172, 185}

A significant report was made that triploid plants yielded more sugar than diploids because the larger roots maintained the same percentage while the diploid tended to reduce the percentage of sugar per hundred grams as the larger-sized beets developed. An additional set of chromosomes raising the number from 18 to 27 did not prove detrimental to volume of sucrose per acre of plants. This represented an important advancement in sugar beet breeding⁶³ (Fig. 13.3).

If triploids were superior — and this has been shown in several cases — then special procedures were required to produce triploid seed. Tetraploid seed parents are made, and then pollinations are carried out with the diploid. Studies by Japanese workers show practical plans for making triploids.²³⁷

The increase in sucrose per unit area of cultivated triploids justified the additional work to make triploids which produce more su-

crose than either diploid or tetraploid, in this case, the 2X or 4X sugar beets. Intervarietal 3X hybrids between high-yielding tetraploids and disease-resistant diploids will prove better than any of the present triploids.

Large-scale production of 3X seed remains a serious problem. However, the self-incompatibility of the species can be used to ad-

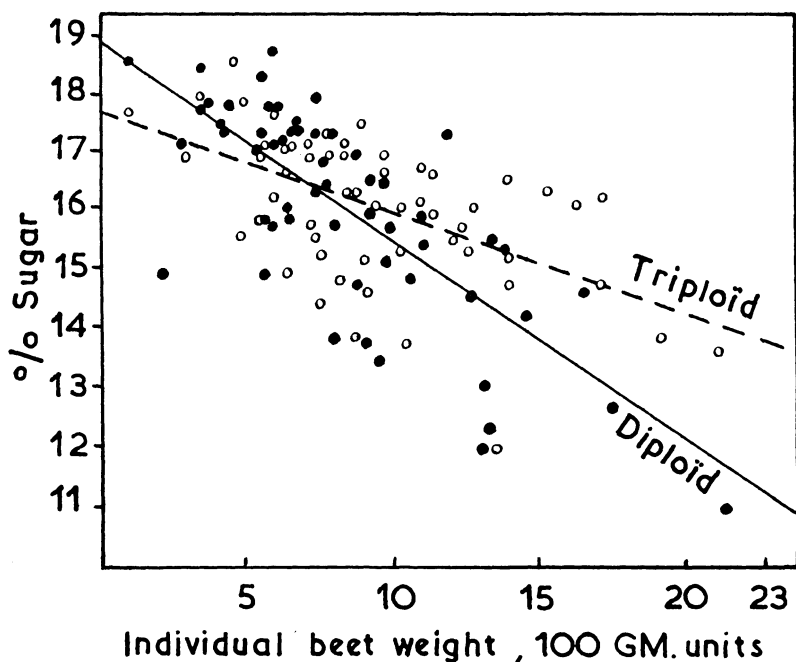


Fig. 13.3—Weight of root and percentage of sucrose production does not decrease at same rate as in diploid when large roots are produced. The addition of another set of chromosomes does not pass the optimum for sugar production per acre. (After Peto and Boyes)

vantage. This alternate planting of 4X and 2X varieties can be used. Seventy per cent of the seeds from the 4X plants are triploid on an open pollination basis. About 30 per cent from diploid are triploid seed. Other factors are involved, such as maturity dates, pollen tube growth, and environment that influences seed production. The optimum number of chromosomes has not been exceeded in the triploid.^{121, 122}

Through the cooperative activities of the National Institute of Genetics Laboratory of Plant Breeding, Hokkaido University, the Hokkaido Agricultural Experiment Station, and the Japan Beet Sugar Manufacturing Company, improvement of sugar beet by means of induced polyploidy has progressed very satisfactorily.²³⁷

The 3X beets are more vigorous; they grow better and always yield more than other beets. Large-scale tests in 1949 and 1950 proved the superiority of the 3X beets.

13.2-3: *Triploid fruits.* Some of the best varieties of apples, Stayman, Winesap, and Baldwin, are widely known. Since giant sports can be produced by colchicine, in similar fashion to the naturally occurring types, the drug has ready application in apple breeding. Triploids can be made from hybrids between tetraploid and regular diploid varieties. These have possibilities for winter hardiness according to tests by special laboratory equipment.⁷¹ Among 31 tetraploids, two varieties were exceptionally hardy. *Malus baccata*, a diploid species, has been polyploidized and might well be the start for breeding stock.

Triploid guavas have been reported occurring in nature. Such types are seedless. Tetraploids induced by colchicine were promising sources for making crosses between diploid and tetraploid.⁸⁶ Assuming that other qualities could be controlled, polyploidy for this economic crop and particularly seedless fruit production should represent an important improvement.⁸⁶

13.3: Monoploids and Autodiploids

The first monoploid plant discovered in 1922 proved that plants existed with one set of chromosomes. More than 30 genera have been added to the list with monoploids reported for one or more species.⁹⁵ The improvement of methods for detecting monoploids is an important part of the program. At once geneticists recognized that doubled monoploids became homozygous diploids. The theoretical and practical use for breeding purposes should not be underestimated. Since the first monoploids were reported, the practical value for homozygous breeding stock to produce hybrid maize has been developed extensively.³¹

The frequencies of the appearance of monoploids are low. Their propagation after isolation from diploid cultures depends upon the doubling of chromosomes in tissues that develop the pollen and egg cells. Colchicine serves adequately for increasing the sectors that double to give rise to fertile tissues. The problem that remains is to find ways to increase the frequency of producing monoploids, applicable to a large number of plants.

A prediction was made that the discovery of methods to increase the frequency of monoploids would mark another period in the history of polyploidy breeding (cf. Chapter 11, Ref. No. 43). According to this scheme the *Drosera* research by Rosenberg marked the beginning; a distinction between allopolyploidy and autopolyploidy was the second phase; and colchicine in 1937 was the beginning of the

third period. Large-scale production of monoploids is a discovery for the future.

The frequency of increasing monoploids has been improved by special methods adapted for a few species. Twin seedlings proved to have a high incidence of monoploids in flax, cotton, and peppers. The monoploids derived from the twin embryo method were isolated and doubled to make the homozygous diploids.^{130, 217} As a basis for improving commercial varieties some application has been made in this direction.²¹⁷ Since many seeds can be run over the germinators, more monoploids are discovered than was possible by field selection. *Gossypium* was treated by these methods.¹⁵

Significant differences in the frequencies of monoploids have been found with certain stocks of maize. Previously selected strains were better than unselected ones. Open-pollinated varieties, generally, were comparatively low for production of parthenogenesis.³¹ By appropriate genetic markers, introduced from the pollen parent, the detection of monoploids at seedling stages is improved. Color genes from the pollinator are expressed in the diploid, but not those from the maternal monoploids. Cytological confirmation of the monoploids among the colorless seedlings proved that the marking system was reliable.

Monoploid sugar beet obtained from seed taken from a colchicine-treated shooting plant has been found. Their occurrence is quite rare. In another instance, the monoploids were derived from colchicine-treated populations. An interspecific hybrid of *Nicotiana* produced two monoploid plants. One of the plants was like one parent, *N. glutinosa*, and the other like *N. repanda*. In the original cross the former parent was the female type and latter was used as the pollinator.

An important use for colchicine arises for making autodiploids from monoploids, thereby increasing the number of plants that can be propagated. By spontaneous doubling some sectors regularly produce viable pollen and eggs. Injecting 0.5 ml. colchicine into the scutellar node of the monoploid seedling proved to increase the amount of good pollen produced, an index of doubling.³¹ A unique feature and application of the autodiploids of maize arises from the fact that genetic systems are fixed as gametes and testable as such. Thereafter the autodiploid reproduces the fixed system of genes.

13.4: Conclusion

The number of autopolyploids is larger than that of the amphiploids. Reference numbers in this chapter and other chapters will be useful to check the many kinds of plants already studied. The volume of literature has developed so extensively that every example could not be

cited in the space allotted. Only selected examples that pointed out principles and basic features about polyploidy were chosen for the text discussion.

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