N.V. TSITSIN

Wide hybridization in plants.

AKADEMIYA NAUK SSSR

N. V. TSITSIN, Editor

Wide Hybridization in Plants

TRANSLATED FROM RUSSIAN

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AKADEMIYA NAUK SSSR. VSESOYUZNAYA AKADEMIYA SEL'SKOKHOZYAISTVENNYKH NAUK IMENI V.I. LENINA

Academy of Sciences of the U.S.S.R. All-Union Academy of Agricultural Sciences im. V.I. Lenin.

WIDE HYBRIDIZATION OF PLANTS

(Otdalennaya gibridizatsiya rastenii)

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Academician N.V. Tsitsin

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Translator's Note

The translators have made no attempt at a uniform treatment of binomial plant names with regard to capitalizing substantive apposites, genitive endings of the specific name and endings of the generic name (Agropyron, Agropyrum). The names have been rendered as given by the different authors of the papers of this collection.

The names of Russian authors have been transliterated in accordance with accepted rules (British Standard), except when quoted as authorities for binomials, in which case their names appear in the Latinized version given in the text.

Some breeding terms which have no English equivalents have been conveyed literally rather than interpreted. Examples are: "form-creative process, shattered heredity, vegetative intermediary, multiple selection."

WIDE HYBRIDIZATION IN VEGETABLE BREEDING

D. D. Brezhnev

First Vice-President of the All-Union Academy of
Agricultural Sciences im. V. I. Lenin

Academician N. V. Tsitsin has dealt exhaustively with the theoretical basis and history of wide hybridization in his report, and this eases our task considerably. We would, nevertheless, like to mention some work having a general theoretical importance, which also touches upon the history of the problem.

Wide hybridization dates from the second half of the eighteenth century, when Koelreuter obtained a hybrid between *Nicotiana rustica* and *Nicotiana paniculata* for the first time.

Academicians Pallas, Gaertner, and Naüdin could be cited among the first workers who obtained data entirely in accordance with Koelreuter's.

Darwin, too, paid considerable attention in his investigations to problems of wide hybridization. He was the first to draw attention to causes of incompatibility, and in his famous work "The Origin of Species" he already stressed both morphological and physiological causes. On causes of non-crossability between species, Darwin wrote: "In the case of first crosses, the greater or lesser difficulty in effecting a union and in obtaining offspring apparently depends on several distinct causes. There must sometimes be a physical impossibility of the male element reaching the ovule, as would be the case with a plant having a pistil too long for the pollen-tubes to reach the ovarium. It has also been observed that when the pollen of one species is placed on the stigma of a distantly allied species, though the pollen-tubes protrude, they do not penetrate the stigmatic surface. Again, the male element may reach the female element but be incapable of causing an embryo to be developed.... Lastly an embryo may be developed, and then perish at an early period". Darwin, Ch. The Origin of Species*.

The interest in a practical utilization of interspecific and even intergeneric hybrids has grown with the development of science and the accumulation of new data. Interest in this problem was largely provoked by the discovery in nature of wild plant species possessing numerous valuable distinguishing characters (disease resistance, cold-hardiness, a high dry-matter content, etc).

* [The source cited in the Russian original is: Darwin, Proiskhozhdenie vidov, pp. 433-434.]

At the end of the nineteenth and the beginning of the twentieth century, Luther Burbank began applying interspecific hybridization to fruit and other cultures.

During this period the scope of investigations in wide hybridization was greatly expanded, thanks, in particular, to the work of our compatriot, I. V. Michurin. He not only demonstrated the possibility of obtaining interspecific and intergeneric hybrids, but developed a whole series of new methods for overcoming incompatibility, and ultimately formulated a sound theory of wide hybridization in plants.

Already in his early articles he noted in wide hybridization "an infinite vista of possibilities for obtaining entirely new fruit species, the form and properties of which are yet unknown" (Michurin, I. V., Sochineniya (Works), 1:422. 1948).

Michurin severely criticized those botanists who maintained that it is impossible to obtain interspecific and intergeneric hybrids; he proposed concrete methods to ensure success in wide hybridization.

The most significant achievements of Michurin and a number of other investigators in wide hybridization were attained in fruit breeding. This advance was mainly because fruit cultures are generally propagated vegetatively, so that the modifications obtained are more readily preserved in the descendants. In other cultures, and particularly in annual grass and vegetable crops, there are numerous difficulties in the production of interspecific hybrids. But in this field also, scientists and practical growers have considered methods of combining certain traits inherent in particular species and genera.

Indeed, the desirable characters of different species and genera, not otherwise occurring together within a single species, can be combined only by wide hybridization. Consider the sensation a tomato - Physalis cross would cause! The fruit being enclosed within a bladderlike calyx, as in the ground cherry, is the one character which would solve the problems of tomato storage and transport. Again, fruits with a high dry-matter and vitamin content might be obtained by bringing together certain characters of peppers and tomatoes. Further, the cold-hardiness of some species might be successfully combined with the superior taste qualities of others, by crossing melon with squash.

In leguminous plants, a combination of the stem characters of beans and peas would facilitate mechanized harvesting of these crops. In addition to being economically valuable, such forms would be scientifically interesting. I. V. Michurin himself said that wide hybridization opens a wide field of activity to original breeding work, as hybrid forms with extremely varied characters are highly adaptable to the external environment of a new locality. The prospect of creating such interesting and useful forms attracts scientifically-minded vegetable breeders, and much attention has been paid to this problem for a considerable time.

For convenience, we will briefly survey wide hybridization achievements, according to groups of crops, omitting the older material.

Interspecific and intergeneric tomato hybrids have been thoroughly investigated in Russia and elsewhere.

The studies of the following workers are noteworthy: O. I. Asfarova-Ryabova (1938), V. A. Borkovskaya (1938), N. V. Tsitsin and M. Z. Nazarova (1953), E. V. Ivanovskaya (1954), K. V. Ivanova (1954, 1957), F. D. Kryzhanovskii (1955), N. A. Solov'eva (1956) and T. B. Batygina (1957).

The following investigations by foreign scientists are noteworthy: G.W. Skirm (1942), P.G. Smith (1944), H.B. Walker (1945), W.A. Frazier (1947), R.E. Lincoln and G.B. Cummins (1949), M. Lesly and J.W. Lesly (1952), McGuire and K.M. Rick (1954), and other workers, who studied wide hybridization in the genus *Lycopersicon* Tourn.

The production of hybrids with economically valuable properties by crossing *L. esculentum* with such tomato species as *L. peruvianum* or *L. hirsutum* is an important problem. The species *peruvianum* and *hirsutum* possess very valuable properties. Both species are resistant to a number of widespread diseases: tobacco mosaic, leaf mold (*Cladosporium fulvum*), septoria leaf spot, and others. Also, *L. hirsutum* is valuable for its frost hardiness (it can withstand frosts to -2°C). Its fruit contains three to four times as much carotene as cultivated tomato fruit. Hence it is valuable breeding material. However it is not easy to obtain hybrids between these species, as they intercross with the greatest difficulty. The production of varieties that possess all the characters listed is particularly difficult.

In 1933, O.I. Asfarova-Ryabova crossed *L. esculentum* and *L. peruvianum* at the Kamennostepnaya Station*, both by using a pollen mixture which was applied repeatedly to the same flower, and also by crossing with polyploid forms. She used these methods to overcome incompatibility, and only succeeded in obtaining one hybrid plant, which flowered abundantly but was almost completely sterile.

Lesly, in 1953, observed that only parthenocarpic fruits with empty nongerminating seed are obtained by crossing the cultivated tomato with *L. peruvianum*.

We are still studying this question with K.V. Ivanova and T.B. Batygina at the All-Union Institute of Plant Cultivation.

In our study, we first had to work out methods of overcoming the incompatibility between *L. esculentum*, *L. peruvianum* and *L. hirsutum*. We used several known methods, such as single, double and triple pollination, pollination with small anther columns, and pollination by mixed pollen.

After three years we concluded that backcrossing and pollination by mixed pollen are the most effective.

The interagent method (used by K.V. Ivanova) is another possibility. The maternal plant of *L. esculentum* was grafted, in its cotyledon stage, onto more developed stocks of *L. peruvianum* (stage of five to six real leaves); later, *L. peruvianum* pollen was placed on the stigmas of emasculated *L. esculentum* flowers for three to four days.

Using all these methods, we obtained sound seed which yielded good seedlings when sown. The seedlings of hybrid fruit were already distinguished by a large variability in shape, size and leaf characters. Moreover, the germination of the seeds was uneven. Later, this same seed was sown near Leningrad and in the Maikop Experimental Station (Krasnodar Territory). In the first and second generations a considerable segregation of characters was observed. Plants of an intermediate type as well as a series of completely new forms were obtained in addition to the two parent

* [State Breeding Station in the Kamennaya Steppe.]

types. On the whole, plants of the seed-parent type* dominated. Thus, in 1953, of 606 hybrid plants sown near Leningrad 453 were of the seed-parent type, 148 of the pollen-parent type, and only five were intermediates.

Hybrid plants of the paternal type proved to be sterile in crosses with L. peruvianum. A high resistance to Macrosporium and Phytophthora was observed in hybrid plants of the seed-parent. The most interesting and valuable feature of these crosses is the appearance of plants of an intermediate type. Among such plants a variable range of morphological characters is observed. It appears that hybrid seed is more easily obtained from L. esculentum × L. hirsutum - with L. esculentum as maternal form - than from L. esculentum × L. peruvianum. From a breeding point of view, L. peruvianum is the more interesting partner.

These investigations show that the segregation of F_1 and F_2 hybrids depends on the conditions under which the F_1 plants germinate. This is very important, as it indicates methods of directing this process.

Similar work has been done by S.S. Voskanyan of the All-Union Institute of Plant Cultivation. She obtained a form of practical value, resistant to Septoria and Macrosporium. This form was selected from hybrids between the cultivated variety Shtambovyi karlik [Dwarf-stemmed] and L. hirsutum.

Workers in other countries have also obtained interesting hybrids in recent years. W.S. Porte and H.B. Wacker (U.S.A., 1945) obtained hybrids between L. esculentum and L. peruvianum by backcrossing.

Like many of their predecessors, these authors failed to obtain seed in a whole series of combinations. Viable seed was eventually obtained by crossing with the Prince Borghese variety. There were forms resistant to Cladosporium and root eelworm among the F_2 plants. In 1953 variety Waltham Mold-proof Forcing was obtained at the Massachusetts Experimental Station.

A number of workers used L. peruvianum for obtaining eelworm-resistant forms: F.A. Romsac (1942), D.E. Ellis (1949), V.M. Watts (U.S.A., 1947); W.A. Frazier and R.K. Dennet (U.S.A., 1949). V.M. Watts obtained resistant forms which were fertile and had small orange-red fruit.

A.F. Jaeger and H.J. Purinton (1946) at the Hampshire Experimental Station also obtained fertile forms with a high ascorbic acid content from crosses between L. esculentum and L. peruvianum. The largest fruits were selected, and their seed sown. The plants obtained were back-crossed to L. esculentum.

The fruit of the F_3 hybrid has a 46 to 67 mg% ascorbic acid content (against 19 mg% in the standard). The result of these crosses was the New Hampshire Victor variety, with an ascorbic acid content of 39 mg%.

Cases of crossing of L. esculentum with L. hirsutum are also known from the literature.

R.E. Lincoln and G.B. Cummins (U.S.A., 1949) crossed L. esculentum with L. hirsutum to obtain Septoria - resistant varieties. They obtained six hybrid generations, but resistance to septoria leaf spot in the obtained forms was less than that of L. hirsutum.

* [Presumably L. esculentum.]

J. W. Lesly (U.S.A., 1948) obtained hybrids that (like L. hirsutum) for several years were hardly ever infected with mosaic.

The practical results of wide hybridization work in tomatoes must be stressed. In 1950, six hybrid varieties were obtained at the experimental station of the University of Honolulu in Hawaii by including L. peruvianum in the crosses. These varieties (Hawaii, Kawai, Lanai, Mani, Molonai, Niihau) were resistant to fusarium and a number of other diseases.

In 1954, the variety Valabond V-508, resistant to nine races of Cladosporium, was obtained at the experimental station of Ontario (Canada) from crosses with L. hirsutum. A number of other disease-resistant varieties which were obtained by wide hybridization are also known.

Inviable seed is often obtained on crossing species of the genus Licopersicon Tourn. There are many careful studies of this phenomenon.

The work of G. Smith (1944) is noteworthy. He observed that the fruits setting from L. esculentum - L. peruvianum crosses had small elongated embryos. From a study of the embryo development he established that the endosperm begins dying off on the 30th to 40th day after pollination, and that later, the embryo itself dies off. Smith found a method of excising the embryo from the seed. These embryos were put into Petri dishes with a nutrient solution and placed in a thermostat at a temperature of 25° C. After two to three days, they were exposed to diffuse light - and, a week later, normal plants began developing from the embryos. Analogous investigations were carried out by G. W. Skirn (1942) and B. Choudhury (1955).

Much research has been done on the crossing of cultivated tomato with lines of the currant tomato (L. pimpinellifolium), which we consider a subspecies. Lines of this subspecies are distinguished by a high dry-matter content (as much as 8 to 10%), a high sugar content and a fair resistance to soil drought and certain diseases.

The utilization of these lines in breeding often gives good results. Daskalov (Bulgaria, 1957) succeeded in obtaining valuable forms from crosses with a line of the currant tomato (cited by him as L. racemigerum). The varieties which he obtained are superior in yield and in additional valuable qualities to other varieties grown in Bulgaria.

Many workers overcome incompatibility in intergeneric and interspecific vegetable crosses by bringing the partners close to each other vegetatively (graft hybrids).

N. V. Tsitsin, F. D. Kryzhanovskii, E. V. Ivanovskaya, and M. Z. Nazarova obtained a tomato - Cyphomandra hybrid. It had been found impossible to cross these genera previously. It was decided to produce hybrids vegetatively. In this vegetative hybridization, the scion was systematically deprived of its leaves and, as a result, a series of morphological and physiological modifications appeared. All these modifications were fully transmitted to the progeny. In the third generation derived from Cyphomandra stock grafted with the tomato variety Bizon, one plant of an intermediate type was obtained. Its seed was fully sound. From 123 seedlings produced, only one plant resembled Cyphomandra. Thus the first intergeneric hybrid was obtained.

It was also I. V. Michurin who began producing new, more highly resistant melon varieties by wide hybridization. Michurin obtained the new, early-maturing melon variety Kommunarka by crossing selected local and Far-Eastern early-maturing, resistant varieties with varieties of European origin. He also carried out crosses between cucumbers, melons and squashes with the preliminary use of graft hybrids, and also crosses with a wild squash - Thladianta sp. As a result, hybrids with fruits of varying shape, size and chemical composition were obtained.

F. Belik (1956) showed that certain melon varieties intercross with the utmost facility, but hybrids obtained from crosses between cultivated melons and wild ones must be further selected and trained. Table water melons cross well with fodder varieties, but are not easily crossed with wild species. These wild species are particularly valuable because of their immunity characters. The various squash species intercross with the utmost difficulty.

N.I. Vavilov made crosses between melons, water melons, and squashes. He did not obtain positive results. He wrote: "The species of the Cucurbitaceae have drifted so far apart in their evolution that insurmountable obstacles prevent fertile hybrids between them..." (Works in Applied Botany and Breeding) *.

It is only possible, as N.I. Vavilov assumed, to obtain hybrids between Cucumis melo and Cucumis trigonus Roxb. (the cultivated and the wild melon species). This is not surprising, as a series of intermediate forms exists between the two.

N.I. Vavilov quotes several unsuccessful attempts to obtain wide hybrids in the Cucurbitaceae. In Becker's experiments with squash-cucumber crosses, one seedless fruit was obtained; in Naudin's crosses between various squash species no hybrid seed was obtained, and the extensive attempts of Locy to cross different species of squash led him to the conclusion that these species are mutually incompatible. But one must not conclude from these unsuccessful attempts that it is impossible to obtain such hybrids. It seems that new methods are required for hybridization here.

A.F. Makarovskii and M.I. Podmogaev (1952), at the Biryuchekutsk Experimental Station obtained a series of hybrids with normal seed. The success in obtaining hybrids can be explained by the fact that, in all the combinations, morphologically balanced hybrids took part, (i.e., forms with a shattered heredity), and that pollination was done by pollen mixtures.

In recent years, extensive research on wide hybridization in the Cucurbitaceae has been done by N.A. Khokhlacheva in the Krasnodar Vegetable and Potato Experimental Station. Crosses between Cucurbita maxima ♀ and Cucurbita moschata ♂ were effected. Khokhlacheva did not succeed in obtaining hybrids in the normal way for a long time. To overcome incompatibility, the preliminary use of graft hybrids was resorted to. The seed-parent form was used as the stock. After bringing partners close to each other vegetatively in this manner, sexual hybrids could be produced. However, the fertility of these hybrids was low in the F_1 and F_2 generations. Maximum segregation was observed only in the F_3 generation, when economically valuable hybrid forms, high-yielding and with a high sugar content, were obtained.

N.A. Khokhlacheva also grafted cucumbers on squashes. In the south, where frequent dry winds reduce cucumber yields, varieties which are resistant to this are required. To obtain such varieties, grafting was

* [Vavilov, N.I. Trudy po prikladnoi botanike i selektsii (Works in Applied Botany and Breeding). — 14 (2), Leningrad, 1925.]

resorted to. On grafting, the cucumber undergoes a series of modifications (particularly if grafted a second time): the inflorescence becomes racemose, flowering starts seven to ten days earlier, and yields increase.

It is desirable to extend melon cultivation northward.

S.P. Lebedeva began her studies in the grafting of melon on squash in 1925. She examined the various grafting methods carefully and selected the best stocks and scions. The most suitable scions appeared to be late and midseason melons from Uzbekistan. The Espeel' variety (S.P.L.) or Podmoskovnaya Lebedevoi, which succeeds well in the Moscow area, is a result of her work.

The success of interspecific and intergeneric crosses can be aided greatly by grafting.

O.V. Yurina obtained the relatively cold-resistant melon varieties Gruntovaya gribovskaya and Gribovskaya rassadnaya 13 by employing vegetative and sexual hybridization in conjunction with each other.

Further studies in wide hybridization between squashes and melons are: V.G. Smirnov and O.A. Smirnova (1939), O. Gashkova (1944). Foreign scientists also give due consideration to these questions in their investigations. Noteworthy among many others are the studies of G.P. Eseltine (1936); J.R. Wall (1954) in U.S.A.; and T.W. Whitaker (1951), who carried out crosses in the genus Cucurbita in an attempt to clarify the origin of C. maxima; J. Jamane (1953), Fakashima (1953) and H. Hayase (1954) in Japan; Batra (1953) in India; Grebenscicov (1955) in the German Democratic Republic; R. Schagen (1956) and F. Weiling (1956) in the Federal Republic of Germany.

Wide hybridization plays a very important part in the genus Allium. As early as 1935, work was begun on crossing the common onion (Allium cepa) with Welsh onion (Allium fistulosum) and Altai onion (Allium altaicum).

In 1935, S.L. Emsweller and H.A. Jones (U.S.A.) crossed Allium cepa with Allium fistulosum. Seven seeds were obtained by hand pollination, and one plant was grown. Morphologically this plant was of an intermediate type; it developed vigorously, was almost completely sterile and resembled A. fistulosum in being perennial.

In the U.S.S.R., A.A. Krivenko and G.V. Fedorov worked on the same crosses. Allium cepa is nonresistant to frost; A. fistulosum is frost-hardy but does not form bulbs. A combination of these two properties* would be of great practical importance. In 1934, G.V. Fedorov obtained 12 viable A. cepa × A. fistulosum hybrids. In 1935 he crossed A. cepa with A. altaicum. F_1 hybrids between the common onion and the Welsh onion or the Altai onion are marked by heterosis. They have very delicate green tops and, as they can be propagated vegetatively, the author recommends the utilization of these F_1 hybrids for onion tops.

A.A. Krivenko's work in wide hybridization of onions merits note. In crosses with common onion he used Welsh onion, Altai onion, chives, and leeks. He carried out reciprocal crosses between the common onion and these latter Allium species. He found that A. cepa is best used as seed-parent, especially the older varieties with balanced characters where there is less influence of the wild forms. Economically valuable forms can be obtained more easily using the older varieties. Accordingly, Krivenko stresses the importance of suppressing certain wild traits, and

* [Bulb formation and frost-hardiness are obviously meant.]

recommends crossing the common onion with wild species in their first year of flowering, and to backcross the F_1 hybrids to the common onion. Stable forms can be selected from the ensuing progeny.

The F_1 Allium cepa × fistulosum hybrid Troitskii mnogognezdnyi [Multilobate], produced by A.A. Krivenko, has a number of desirable characters: it is perennial, frost-resistant, high-yielding and of pleasant taste. It was approved for market cultivation in 1940.

The achievements of wide hybridization in legumes are also notable. Nonlodging pea forms suitable for mechanized harvesting, immune varieties, extra early-maturing ones, etc, can be produced. K. Tjebes (Sweden, 1927), M.M. Sasonkina (1935), Sousa Bourdouil (1938), V.V. Novikov (1939), M. Shel'khorn (1940), Lamprecht (Sweden, 1941, 1952), P.I. Shul'ga (1952), S. Honma (U.S.A., 1955) and Buishand (Netherlands, 1956) have worked on this subject.

Wide hybridization in legumes has been studied in detail from 1936 to 1940 by V.V. Novikov. He pollinated Vicia faba with a mixture of pollen of other Vicia species when direct crosses of peas with the broad bean did not succeed. In 1937, crosses between broad bean, winter vetch (Vicia villosa) and common vetch (V. sativa) led to the production of intermediate forms, which were further utilized for crossing with peas (with pure lines or with the hybrid Alaska × Capital). From these crosses three valuable forms were obtained: 1) a nonlodging, high-yielding pea-bean; 2) an immune form of pea-bean; 3) an extra early-ripening form of pea-bean, which completes its vegetative growth within 54 days.

M.M. Sasonkina made use of preliminary grafting for producing hybrids between Lupinus polyphyllus and the garden pea (Pisum sativum), Lupinus polyphyllus and the field pea (P. arvense), Lupinus angustifolium and the garden pea, and many others. Field pea × Lupinus polyphyllus and field pea × L. angustifolium hybrids were obtained from crosses made after double grafting. Nonlodging pea forms and alkaloid-free lupine forms might have resulted from further investigations in this direction.

The work of A.M. Drozd (at the Crimean Experimental Breeding Station) in wide hybridization involving kidney bean is also of great interest.

A.P. Lorts (U.S.A., 1952) studied hybrids between lima bean and the wild species Phaseolus polystachyus. Crosses were made with the object of introducing into the lima bean such valuable traits as underground germination and resistance to various diseases. After numerous attempts, seven hybrid plants were obtained, in all of which the cotyledons remained underground during germination.

Much work has been done on intercrossing species and genera of the Cruciferae in the U.S.S.R., as in other countries. G.D. Karpechenko (1937 to 1938) intercrossed Brassica oleracea, Br. chinensis and Br. carinata, and obtained fertile hybrids.

A detailed study of F_1 hybrids between cabbage and radish is being made in Japan by Fukushima; the first Brassica oleracea × Raphanus hybrids were obtained in the U.S.S.R. by G.D. Karpechenko.

In Hungary, A. Kiss (1956) experimented with hybridization between rape (Brassica napus) and turnip (Brassica rapa).

An intermediate (rape × cabbage) hybrid fodder plant called "rapko" was obtained in Germany in 1936.

The work of R.A. Calder (New Zealand, 1937), on pollination in the genus *Brassica*, should be noted. He showed that rape (*Brassica napus* L.), turnips (*Brassica rapa* L.),and swedes (*Br. napobrassica* Mill.) can intercross under natural conditions, but that none of these species intercrosses naturally with *Brassica oleracea*. This must be taken into account in work with these particular species, as under natural open cross-pollination the seed is apt to become contaminated. Plants for seed-growing have to be rigorously isolated. Work on interspecific *Brassica* crosses is being done in China (Tsai I-sin', 1955). All these studies are accompanied by extensive cytological investigations.

G.S. Voskresenskaya has sent a communication about mustard, rape, and common winter cress (*Barbarea vulgaris*)- cabbage hybrids, obtained in the Institute of Oil and Essential Oil Crops*.

Note should be made of work being done on the interspecific hybridization of red peppers by Swami Rao R., M.R. Narasimaha Rao, and T.V. Subramanian (India, 1942), and on interspecific crosses involving eggplants by T. Tatebe (Japan, 1941). R.C. Thompson (U.S.A., 1943) worked on interspecific hybridization in the genus *Lactuca* with the purpose of elucidating genetic relationships between species.

This brief and incomplete survey shows that work on wide hybridization in vegetable cultures is being done by many scientists in the U.S.S.R., and in other countries. One can now list dozens of vegetable crop varieties obtained in this way. It is true that work on the wide hybridization of vegetable cultures is accompanied by considerable difficulties. In fruit, the modifications obtained are easily preserved in the clonal, vegetatively propagated descendants; vegetables, on the other hand, are almost invariably propagated by seed. Yet these difficulties are not insurmountable.

In work on wide hybridization, obstinacy and, above all, patience are important. This was stressed by I.V. Michurin. All work should be carried through to the end and not be left half-finished, as has often happened.

Our investigations on wide hybridization are one-sided. The crosses are made, but the resulting hybrids are rarely trained. The dominance of characters can be modified and guided in the desired direction by clever training. Almost no cytological and embryological studies of interspecific and intergeneric hybrids have been made in recent years, although these most essential investigations could be of great help in discovering reasons for incompatibility, sterility, and so on.

Success of crosses often depends on the conditions under which the parental forms were grown, but there are almost no investigations of this.

The method of raising embryo cultures of interspecific and intergeneric hybrids on an artificial nutrient medium is not utilized at all. In many cases hybrids between wide forms could be obtained much more easily by this method. More consideration should be given to the possible use of radiation of both hybrid seed and parental forms, to increase the viability of intergeneric and interspecific hybrids.

Future studies on vegetable cultures should take note of all these shortcomings. More publicity should be given to current investigations on wide hybridization. Research projects should be developed on a larger scale, and be carried out more competently, in conjunction with cytologists, embryologists, biochemists and physiologists, and with full consideration for the achievements of modern science.

* [Institut maslichnykh i efiromaslichnykh kul'tur.]

METHODS OF WIDE HYBRIDIZATION IN POTATO BREEDING

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Wide hybridization in potato-breeding is characterized by the diversity of species which can be used. It comprises interspecific hybridization between certain cultivated potato species and hybridization between cultivated and many wild potato species.

The degree of variability among potato species, whose number is about 200, is not only determined by a diversity in morphological-systematic features. The range of variability in characters, resulting from the remoteness of the phylogenetic links between the species, constitutes a basis for the division of potato species of section Tuberarium, genus Solanum, into 22 series (Figure 1). The distance between these series is also confirmed by cytological data.

Some of the more primitive series are represented by diploid 24-chromosome species - the series Etuberosa, Juglandifolia, Morelliformia, Pinnatisecta, Circaeifolia, Polyadenia, Vaviloviana, Cuneoalata, Megistacroloba, Glabrescentia (a total of ten series). Some series are represented by both diploid and triploid species: Bulbocastana, Cardiophylla, Commersoniana. In species of the series Longipedicellata and Tuberosa, there are triploid and tetraploid species. In series Piurana and Oxycarpa only tetraploid species are known. Series Rotata contains some tetraploid species among a great majority of diploid species. In series Acaulia, triploid and pentaploid species of hybrid origin derive from a tetraploid starting species. Hexaploid species occur in only two series. One of them, series Conicibaccata, contains diploids, tetraploids, and hexaploids. Series Demissa, on the other hand, has no tetraploids, but contains pentaploid species.

The cytological "flexibility" of the potato species facilitates the creation of large numbers of artificial polyploids; this has been used in work with many species (N. A. Lebedeva). Artificial polyploids transgress beyond the natural polyploid range of potatoes; entirely viable octoploids and dodecaploids have been obtained (S. demissum with 144 chromosomes).

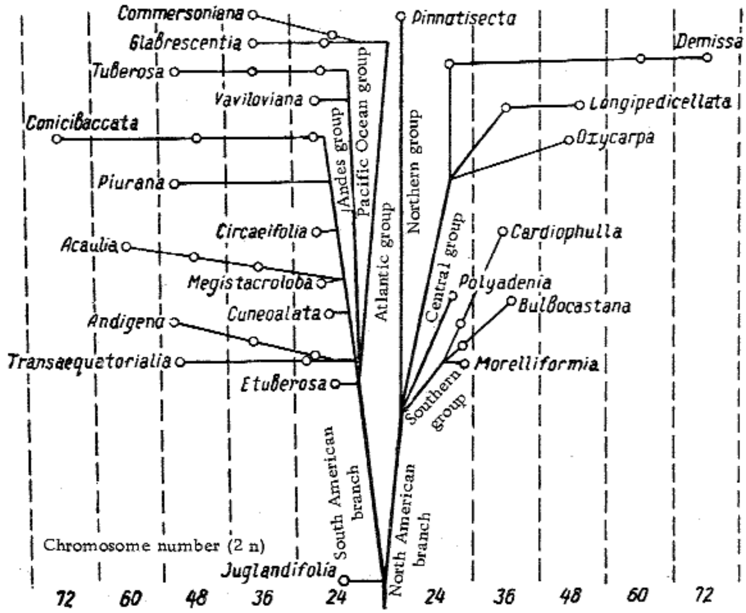


FIGURE 1. Scheme of the phylogenetic system of series of potato species

The cytological differences between potato species are not limited to the chromosome number. Even within the same series, species differ from each other in chromosome morphology and in heterochromatin indices. Potato species also exhibit differences in anatomical and biochemical characters; this is particularly important for breeding.

In a study of the evolution of potato species, the anthocyanidin contained in the species is of particular significance (Dodds, Long, 1955). In 12 diploid, triploid, tetraploid, and hexaploid wild species investigated belonging to seven different series, anthocyanidins were only present in the form of the glycoside petunidin. In three cultivated diploid species, there were another three pigments in addition to petunidin: the glycosides paeonidin, pelargonidin and cyanidin. The last three types are also found in a fourth diploid, S. yabari, which however contains no petunidin. Petunidin was present in 20 other species examined (only "red" phenotypes were investigated). The tetraploid S. andigenum, which probably originated from one of the mentioned diploid cultivated species, contained only petunidin, paeonidin, and pelargonidin. Cyanidin was absent (in contrast to the examination of the diploids, only tubers were investigated here). In S. tuberosum, the glycoside malvidin occurs in addition to these three types.

It is remarkable that only the two pigments petunidin and paeonidin are present (in tubers) in the three triploid cultivated species which originate from different tetraploid species and, in the case of S. Juzepzcuki, from different series. Possibly all these species originated from the diploid S. phureja, which has not been investigated and which should, in this case, also contain the two mentioned pigments.

Differences between the structure of glycoalkaloids, which determine the resistance to Colorado beetle damage, have also been established in the different series. Solanin, the glyco-alkaloid of series Tuberosa, is replaced by demissin in the species of series Demissa, and by solacaulin in series Acaulia. In series Polyadenia and Glabrescentia, glycoalkaloids which have not yet been investigated have been established (Schreiber, 1956); one of these is chakonin. The series of potato species are very remote from each other geographically. They are distributed from Chile to Mexico and the U.S.A. and from the Pacific to the Atlantic coast of America.

The species' distribution areas within each particular series differ markedly in their ecological conditions; this is partly explained by the considerable vertical zonation of the distribution of potato species, ranging from zero to 4,400 m above sea level. Some of the new problems in potato breeding, such as immunity to diseases and pests, frost resistance, adaptability to high temperatures, and modification of the biochemical composition, are a consequence of the diversity of the potato species. In one novel method using potato starting material in interspecific hybridization, ever-increasing importance is given to the creation of hybrids between three and more species, i.e., composite hybrids.

The first question in interspecific hybridization between potatoes is that of compatibility between the species. The elementary question of the importance of the chromosome number in compatibility between potatoes has been solved paradoxically. Species of one chromosome level, for instance species of the series Acaulia, Longipedicellata, and Tuberosa, intercrossed with great difficulty, sometimes with even greater difficulty than did species of this series with others having a lesser number of chromosomes. In some cases, morphological-physiological peculiarities of the flower, such as the short pollen tubes in Acaulia, added to the difficulties in crossing caused by the genetic remoteness between species.

The fact that differences in chromosome numbers seem to be of no negative significance for the compatibility between potato species can be partly related to the "lability" of the polyploid range in the potato. This lability can have a positive influence on the compatibility between species of different chromosome levels.

One of the outstanding instances of heightened compatibility between species of different chromosome numbers is crossability through the agency of unreduced gametes. This occurs in crosses between species of the series Longipedicellata and Tuberosa, between diploid Andigena and tetraploid Acaulia and Tuberosa, and, apparently, octoploid Acaulia. In this last case, the artificial polyploids created greater differences in the number of chromosomes, which improved compatibility. But the general aim in using polyploids in potato breeding is to obtain material with equal chromosome numbers and so improve the chances for successful crosses.

Of great importance in potato breeding are Michurin's methods of overcoming incompatibility - the establishment of a preliminary vegetative contact, the use of pollen mixtures, multiple pollination, and the use of intermediaries.

The search for appropriate methods ensuring the viability of the hybrid progeny is a second problem in interspecific hybridization of the potato. In the large majority of cases, the interspecific first-generation hybrids are at first normal and viable. Cases of malformation and chlorosis are relatively rare. In the second generation, inviable forms increase in number among both interspecific hybrids and backcrosses, in particular in crosses between genetically remote species.

Inviability manifests itself in various stages: failure of the seed to germinate, chlorosis of the cotyledons, different malformations and reduced vigor. As a result of this last, the plants are more susceptible to some virus diseases, mainly, apparently, to virus K. Because of these reasons (reduced vigor), inbreeding has been little used as a direct method for obtaining varieties. The obtaining of potato varieties from first-generation interspecific hybrids is only practicable in cases where two cultivated species are intercrossed which belong to the two different, but closely related series Tuberosa and Andigena. All the old and commonly grown potato varieties belong to the species S. tuberosum L. sens. str. and originate from intervariety hybrids of this species.

The possibility of obtaining varieties from first-generation hybrids between series Tuberosa and Andigena is explained by the fact that the cultivated species of series Andigena do not have many of the negative characters inherent in wild species. The negative characters of the cultivated potato species of this series are mainly the requirement of a short day for tuber formation and, apparently, as a consequence, a decreased yield capacity in our latitudes. Other negative characters of Andigena are only met with in part of the forms and can be eliminated by careful choice of the starting material. They are the intensive coloring of the tubers, blue tuber eyes, sometimes a high content of solanin in tubers, etc.

S. andigenum is used in breeding varieties with a high starch content, varieties with a high resistance to Phytophthora by virtue of a longer incubation period of the latter, and varieties with a barrier resistance to virus X, a resistance to crinkle and, particularly valuable, immunity to the potato eelworm.

Diploid cultivated species, tubers of which have no dormancy period, are used for obtaining varieties yielding two harvests. Here, it has to be taken into consideration that first-generation hybrids may be either tetraploid (owing to unreduced gametes) or triploid. The triploids are under the adverse influence of an unbalanced number of chromosomes and, because of their low viability, succumb to virus diseases within a short time.

By interspecific hybridization between S. tuberosum and S. andigenum, the varieties Imandra, Igarskii, Marii Khrennikovoi, Karagandinskii, Dolinskii, Mikhnevskii, and Mil'da were obtained, as well as other northern varieties, and also a number of foreign varieties, in particular the Netherland varieties which have a high starch content and are resistant to potato eelworm.

By interspecific hybridization of S. tuberosum with the diploids S. boyacense and S. canarense, varieties Khibiny 3, Khibinskii dvuurozhainyi [Khibin Two-Harvest], Khibinskaya skorospelka [Khibin Quick-Ripening], and Shuntukskii dvuurozhainyi [Shuntuk Two-Harvest] were obtained, which yield two harvests per year; a number of promising new hybrids also resulted from this cross.

In breeding work with wild potato species, among which S. demissum is particularly widely used, a great number of adverse characters persist in the first generation and, as a rule, also in backcrosses to S. tuberosum; accordingly no varieties can be produced from this material. Entirely acceptable varieties can only be obtained in composite three-step backcrosses to S. tuberosum (as recurrent parent). Among the obtained varieties (one quarter hybrids) are Fitoftoroustoichivyi

[Phytophthora-resistant], Petrovskii, Krasnoufimskii, and Ural'skii. Many of the Phytophthora-resistant varieties are produced by four-step or even more complex backcrosses. Examples are the varieties Kameraz, Agronomicheskii, Zven'evoi, Zazerskii, Partizan, Uktusskii, and others.

Most of the more than twenty foreign Phytophthora-resistant varieties were obtained by stepwise composite backcrosses to S. tuberosum. In addition to consecutive backcrosses, interhybrid crosses are used, or the hybrids are preliminarily inbred. Abroad, S. demissum is sometimes introduced into crosses with S. tuberosum in the form of preliminarily obtained tetraploid hybrids between S. demissum and diploid cultivated species. In addition to S. demissum, the hybrid species S. semidemissum, and also species of the series Longipedicellata are used in the production of Phytophthora-resistant varieties.

In breeding varieties that are resistant to damage by Colorado beetle and Epilachna chrysome, species of the series Glabrescentia and Commersoniana are used. Species of series Acaulia are used in breeding for frost resistance. Of other species that have some limited utilization, S. leptostigma is used in breeding for increased starch content and S. curtilubum for the same purpose and for the production of frost-resistant varieties.

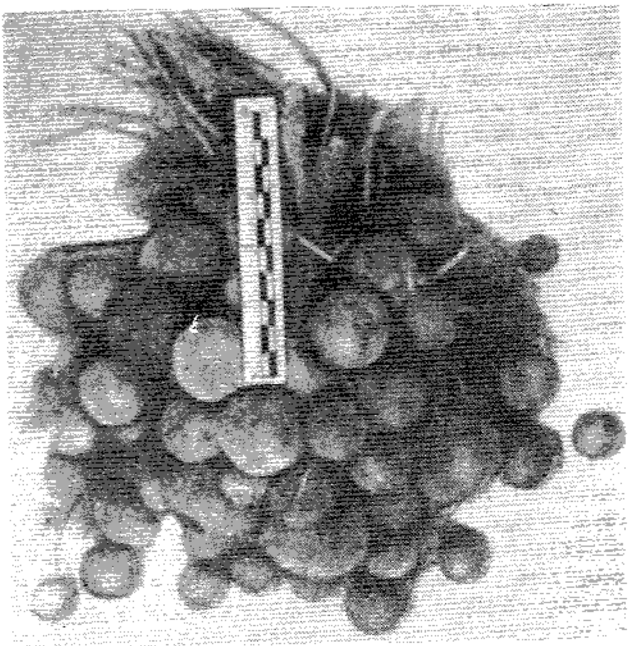
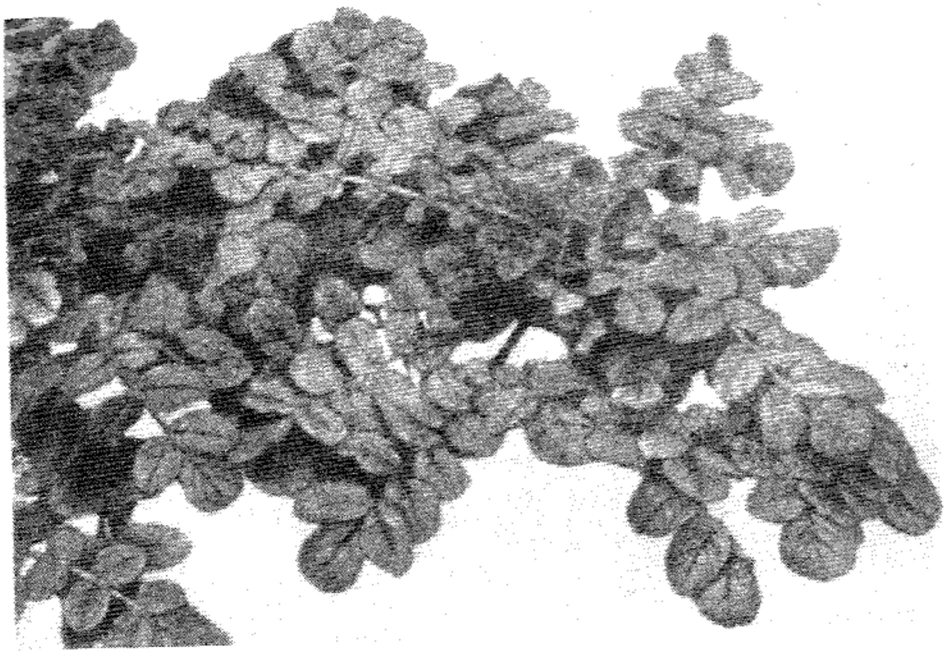


FIGURE 2. Tubers of Solanum rybini

Three-species hybrids, into which one of the three cross components may have been introduced to facilitate crossability (as an intermediary) also have their uses per se, with each of the three components adding to the combination of desirable characters. Since species of hybrid origin, such as S. semidemissum, are natural hybrids between two species, their hybrids with other species can also be considered as three-species forms. Examples of three-species hybrids are 4669/39 Ikkh (a hybrid between S. tuberosum, S. demissum, and S. rybinii), 96-5/s48 from the Rusinovich Station (a hybrid between S. tuberosum, S. demissum, and S. leptostigma), and the All-Union Institute varieties Detskosel'skii and Volkhovskii (hybrids between S. demissum, S. andigenum, and S. tuberosum); all these varieties are resistant to Phytophthora.



Abroad, Phytophthora-resistant varieties have been developed from three-species hybrids between S. tuberosum, S. demissum, and S. andigenum, and S. tuberosum, S. Antipoviczii and S. andigenum. Some hybrids derived from S. Antipoviczii are highly resistant to virus U and resistant to virus A: other three-species hybrids are obtained by crossing two interspecific dihybrids. An example is variety 44335/I30 (S. demissum × S. tuberosum) F_3 × (S. tuberosum × S. andigenum) F_2, which is resistant to the crinkle virus.

Some of the three-species hybrids between S. tuberosum, S. demissum, and S. antigenum, in which there are five to six backcrosses to S. tuberosum, showed a resistance to both crinkle and virus U, and single clones also to virus A. At the same time, they gave satisfactory yields, and sometimes higher yields than ordinary varieties (Rudor 1954, Zuchter Nos. 2/3).

Four-species hybrids between S. tuberosum, S. demissum, S. Antipoviczii, and S. andigenum with two to three backcrosses to

S. *tuberosum* were created for a complex resistance to *Phytophthora*, virus A, and virus U, and a yield ability exceeding that of a number of other varieties.

The above-mentioned four-species hybrids are not resistant to one of the most common viruses, virus X. Only S. *acaule* × S. *tuberosum* hybrids which are backcrossed to S. *tuberosum* five to six times possess this resistance.

Therefore, if varieties, which are simultaneously immune to *Phytophthora*, wart disease (*Synchytrium endobioticum*) and the four most common viruses (X, U, A and crinkle) are to be developed, the mentioned four-species hybrids have to be crosses with the above S. *acaule* × S. *tuberosum* hybrids (Figure 3), the latter being resistant to virus X, virus A, crinkle, harmful races of *Synchytrium* and to some extent to virus U, but not to *Phytophthora*. The creation of five-species hybrids is rendered more easy by the dominance of characters determining resistance to viruses X and U and to eelworm.

HYBRIDS BETWEEN JERUSALEM ARTICHOKE AND SUNFLOWER

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Parental species and their compatibility. For hybridization with sunflower, we have used certain species of the genus Helianthus L., which differ markedly from the former in their morphological characters and general growth habit. In addition to tuberous species of this genus, such as H. tuberosus, H. macrophyllus, and H. subcanescens, we also introduced species with rhizomes or root suckers (H. Maximiliani, H. mollis, H. laetiflorus, H. tomentosus, and others) into the crosses.

Hybridization experiments showed that the group of rhizomatous species with a chromosome number equaling that of sunflower (2n = 34) did not cross at all with the sunflower, whereas the tuberous group with a chromosome number of 2n = 102 crossed relatively easily. H. subcanescens crosses particularly well with sunflower, and H. macrophyllus and H. tuberosus somewhat less easily. Crosses succeed if these species are used as seed parents, while sunflower used as seed parent has an adverse effect on the cross.

We had, and now have, large numbers of first-generation hybrids between sunflower and tuberous Helianthus species at our disposal. The varieties introduced into the crosses include sunflowers from the Don Oil Crop Station (Zhdanovskii 8281) and also from the All-Union Institute of Oil and Essential Oil Crops (Nos. 1646, 6540, and others). One of the Jerusalem artichokes used was Belyi Kievskii [White Kiev], which is distinguished from other varieties by a high fertility under the conditions of the central belt of the Ukraine. The hybrids from its cross with sunflower exhibit a high degree of heterosis, both in aerial mass (silage) and tubers. In recent years, other varieties of Jerusalem artichoke have been introduced into the crosses: Belyi urozhainyi [White Yielding] Ukrainskii 76, S-12-37, and G-71-39, but these are poorly fertile and cross very badly with sunflower.

Form-creative process in hybridization of Jerusalem artichoke with sunflower. The first-generation hybrids are marked by a high variability in all morphological characters, particularly in stem branching, a cordate or ovate leaf shape, tuber formation or absence of it, anthocyanin coloring of the stem, etc.

Hybrid plants can be distinguished from non-hybrids already in the seedling stage by their cotyledons. In ordinary seed-grown Jerusalem artichoke these are dark green in color, more elongate, and without an abrupt transition to the petioles. The cotyledons of the hybrids are intermediate between those of Jerusalem artichoke and sunflower: they are wider, and their blades narrow abruptly where they join the petiole.

The first-generation hybrids between Jerusalem artichoke and sunflower exhibit an intermediate branching type, they are less branched than Jerusalem artichoke, and sometimes entirely unbranched. Among 931 hybrid plants, for example, which we studied in 1956, 61 or 6.6% were unbranched and 332 or 35.6% slightly branched, while 349 or 37.5% had a medium branching habit, and 189 or 30.3% were strongly branched.

The leaves of the hybrids are generally wider than those of Jerusalem artichoke, and vary greatly in size; frequently they are even larger than sunflower leaves. The leaf (petiole) base is usually pithed, a feature used for determining the hybrid nature of the plants.

The leaf petiole is thicker than in Jerusalem artichoke, and thinner than in sunflower. While the sunflower petiole is unwinged and that of Jerusalem artichoke winged to the base, that of the hybrids is almost invariably winged, but to varying degrees, generally to half-way down.

A distinguising mark of Jerusalem artichoke, and in particular of variety Belyi Kievskii, is the red-brown anthocyanin coloring of the stem, particularly of its upper part. In sunflower, there is no anthocyanin coloring. Sunflower × Jerusalem artichoke hybrids segregate markedly for this character and range from intensely colored forms to others which have no coloration at all. Among 940 hybrids studied by us for this character, 379 or 40.3% were anthocyaninless, 142 or 15.1% were weakly colored, and 143 or 15.3% had a strongly colored stem. These data show that the majority of hybrids are intermediate for this character*, while there are few forms with an intense coloring of the stem.

The head diameter in Jerusalem artichoke is fairly small, reaching 1.2 to 1.5 cm, and the heads have no ligulate florets. In hybrids between Jerusalem artichoke and sunflower the head is considerably larger than in Jerusalem artichoke, but smaller than in sunflower; it usually has a diameter of 4 to 5 cm, and 8 to 10 cm in only single specimens. The number of ligulate ray florets is usually intermediate, about 20 to 24. They are intensely yellow, sometimes very large, and often even hang down on the disk.

Fasciations are of frequent occurrence in first-generation hybrids. In certain years, fasciated types are very numerous. Fasciations appear in the form of elongate, double and even triple heads, small heads around the stem, and groups of heads in the leaf axils.

In 1956, the fasciated types were particularly numerous. Among 940 F_1 hybrids, 228 or 24.2% were fasciated plants.

In the second generation the formative processes are even more pronounced. Side-by-side with unbranched forms, there are strongly branching forms, moreover there are modifications in branching habit, and frequently plants appear which do not resemble their parents and are sometimes unlike any representative of the genus H e l i a n t h u s L. in general growth-habit.

* [Sic. This conclusion is not borne out by the figures quoted.]

Segregation also becomes more pronounced in a number of other characters: leaf shape, anthocyanin coloring, increase in head size, appearance of ornamental forms, etc.

According to the heredity of morphological characters, and depending on the dominance of certain traits we divide all hybrids of the first and more advanced generations into five basic types.

FIGURE 1. Hybrids between Jerusalem artichoke and sunflower; of the sunflower - Jerusalem artichoke type with a dominance of sunflower characters.

Type I - the sunflower type. This comprises plants resembling sunflower, which are single-stemmed, unbranched, have a relatively large head, and large cordate leaves of the sunflower type.

Type II - the sunflower - Jerusalem artichoke type. The plants of this type are intermediate, but approach the sunflower group. They comprise weakly branched forms and plants with the branching habit of wild sunflower forms (branching in upper part) with a relatively large head, and more or less cordate leaves (Figure 1).

Type III - the Jerusalem artichoke - sunflower type. In this type we class intermediate plants in which characters of tuberous species dominate. The plants branch quite abundantly, as in the Jerusalem artichoke type (along the entire stem or in its lower part), the head is of a reduced size, some of the stems and leaf petioles are slightly pithed.

Type IV - The Jerusalem artichoke type. This group comprises plants in which Jerusalem artichoke characters are almost entirely dominant.

Type V - the "new forms" type. To this group we refer plants which bear no resemblance to their parents, i.e., which exhibit new characters and sometimes traits which are not inherent in the genus Helianthus; they include plants with an original branching habit, ornamental sunflower-like heads, original leaf shapes (tridentate, lanceolate, and others), etc., (Figure 2).

In first-generation hybrids, plants with intermediate characters predominate, i.e., plants of types II and III. In the second and advanced generations, the number of plants resembling sunflower increased, i.e., types I and II, and also the number of hybrids with new characters, i.e., type V.

The tuber-forming ability of Jerusalem artichoke × sunflower hybrids. Hybrids between Jerusalem artichoke and sunflower exhibit a varying tuber-formation ability. Together with high-yielding plants producing up to 4 kg of tubers each, there are others which only yield 100 to 200 g. The tuber-formation character is dominant in F_1 hybrids.

Only a small percentage (about 1%) of the large number of hybrid seedlings raised by us had an annual life cycle, i.e., the plants were without tubers and other perennial organs (stolons or root buds). A higher percentage of annuals only appeared in single years. In 1949, for example, we had 202 plants in the nursery of first-year hybrids. Among them there were only 8 plants, or 3.9%, with annual life-cycles. The remaining 194 hybrids were either tuberous or had perennial root buds. Seven plants, or 3.4%, had such root buds.

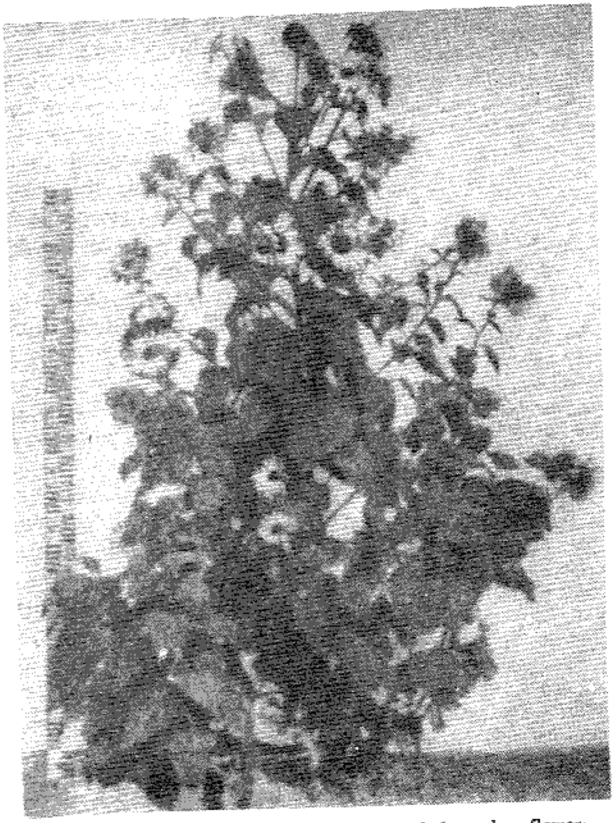

FIGURE 2. Hybrids between Jerusalem artichoke and sunflower; of the "new forms" type

Characteristically, a certain percentage of plants grown from hybrid tubers do not form tubers themselves, though they do not differ from tuber-forming plants in any other way. Twenty-three of 470 plants raised from tubers, or 4.8%, were non-tuberous, and 14 plants, or 29%, formed perennial root buds, or small stolons without tuber thickenings in the collar region.

In the second generation raised from a backcross of F_1 hybrids to sunflower, there were fewer tuberous segregants and more annual types, i.e., the tuber trait appeared as a recessive character.

It has been demonstrated by experiments that the percentage of tuberous segregants can be increased to almost 100% by backcrossing F_1 hybrids to a recurrent tuberous species. The tuber trait is closely linked with the growth habit of the tuberous species, and one can foretell in preliminary assessment whether a particular hybrid is likely to form tubers.

The shape of the tuber is highly variable and ranges from deformed stolon-like types to tubers of an even, potato-type shape. Irregularities in tuber shape constitute an undesirable character in most of the hybrids; the tuber becomes lengthened and develops variously sized outgrowths. We have tentatively established ten types of hybrid tubers.

Vegetative period and fertility of Jerusalem artichoke × sunflower hybrids. Under the conditions of the central belt of the Ukraine the Jerusalem artichoke does not flower at all. It forms buds or late flowers only in rare years with a long warm fall, but forms no seed. The sunflower has a relatively short vegetative period, flowers round about July, and ripens in August. The vegetative period of the sunflower from germination to flowering is 65 to 68 days, and from the seedling stage to ripening 112 to 115 days.

F_1 hybrids have an intermediate vegetative period; most hybrids flower, but relatively few reach seed maturity.

Hybrids between the wild tuberous species H. subcanescens (Gray) Wats. and H. macrophyllus Willd. flower early and reach full maturity in the Ukraine.

The second generation segregates markedly for length of the vegetative period, and its hybrids range from extremely quick-ripening to nonflowering forms.

The hybrids have been divided by us into four groups by fertility, from highly fertile to sterile. The highly fertile group comprises hybrids from the cross between H. annuus and H. macrophyllus. This combination has yielded over 600 achenes per plant in certain years. Hybrids from the cross between H. subcanescens and H. annuus were less fertile. They gave an average of 80 to 100 achenes per plant. Hybrids between the cultivated Jerusalem artichoke (H. tuberosus L.) and sunflower were weakly fertile and almost sterile; on the average, they produced one achene per head or a fraction of one per plant.

The F_2 hybrids from a backcross of F_1 to sunflower or Jerusalem artichoke are completely sterile. We have examined some ten thousand heads, and only in some of them were single achenes formed. As an exception, we obtained a hybrid in 1954 which developed 700 achenes per plant. No cytological study of this hybrid was made, and we can give no reasons for its high fertility. Thousands of other plants from the same cross were totally sterile or produced 1 to 2 achenes per plant. The seeds of this hybrid served as starting material in breeding for rust immunity in sunflower (Figure 3).

Jerusalem artichoke × sunflower hybrids as valuable dual purpose fodder plants. In breeding work with hybrids between Jerusalem artichoke and sunflower we obtained two hybrid clones, No. 15 and No. 120, which have a considerable interest as highly productive fodder plants with a double use (tubers and herbage). Under favorable conditions, plants of both clonal lines reach a height of 3.4 to 4 m and give a high yield of green matter which is suitable for silage, as well as a high tuber yield suitable as fodder for all farm animals, especially pigs.

Under good growing conditions, clonal line No. 120 yielded 300 to 400 centners of tubers and 600 to 700 centners of green matter per hectare in favorable years. The tuber yield from clonal line No. 15 was usually equal to that from the parent variety of Jerusalem artichoke, which is 150 to 180 centners/ha. in the forest-steppe of the Ukraine. In herbage yield, the hybrid clonal line surpassed Jerusalem artichoke considerably. Under ordinary growing conditions, it yielded 600 centners/ha of green matter and, in low lying places, where there is no water shortage, 800 and 900 centners/ha.

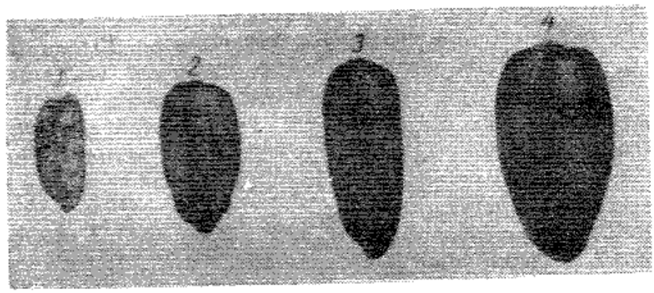

FIGURE 3. Achenes of parents and hybrids
1 - achene of Jerusalem artichoke; 2 - achene of F_1 hybrid
3 - achene of F_2 hybrid; 4 - achene of sunflower.

The aerial mass of hybrid clone No. 120 is somewhat coarse, but the presence of high amounts of carbohydrates (up to 15% of the fresh weight) and other nutrient substances in the stems makes it a suitable raw material for silage.

N. F. Chebotarev (1952) made a comparative study of our hybrids with other crops of fodder importance at the Poltava Research Institute for Pig Breeding*. He gave the following sampling data of fodder units and digestible protein per hectare: hybrid clone No. 120 - 23,190 fodder units and 720 kg of digestible protein, potato - 7,030 fodder units and 120 kg of digestible protein, sunflower - 5,720 fodder units and 410 kg of digestible protein, corn (with cobs) - 6,550 fodder units and 160 kg of digestible protein.

The fodder value of these hybrids' green matter equals that of corn and is higher than that of sunflower greens used for silage. According to determinations made in the Biochemistry Laboratory of the former Institute of Genetics and Breeding of the Academy of Sciences of the Ukrainian SSR, the stems of the hybrids have a considerably higher sugar content than those of sunflower; their sugar content is the same as that of the stems of Jerusalem artichoke. The protein content of the stems of the hybrids is somewhat lower than in sunflower, but no lower than in Jerusalem artichoke; this is seen from the following data (in percentages of fresh weight):

Table

	Carbohydrates	Crude protein
Sunflower Zhdanovskii 8281	5.5	14.6
Jerusalem artichoke Belyi Kievskii	34.4	11.9
Hybrid clone No. 120	32.4	11.9

* [Poltavskii nauchno-issledovatel'skii institut svinovodstva.]

The stems of the hybrids have a high carotene content - 106.8 mg per 1 kg of fodder - and constitute a good raw material for silage. The tubers of the hybrids have a higher fodder value than those of the ordinary Jerusalem artichoke; according to determinations of the same laboratory, the hybrid tubers contain almost 5% more fructoses (of the basic carbohydrate) than the parent variety of Jerusalem artichoke.

The protein content in the hybrid tubers was the same as in Jerusalem artichoke and amounted to 11.3% of the dry substance. The content of minerals in Jerusalem artichoke was 5.1% and in hybrids 4.85%. Because of this mineral content, young pigs fed on these tubers do not develop anemia.

Experiments carried out in the state farms of the Khar'kov and Poltava Regions have demonstrated the value of this crop for pig-breeding farms. The green mass of the hybrids was harvested and silaged by the state farms in the fall, and the tubers were left in the ground over winter and used for pig grazing in early spring.

In the pig-breeding State Farm No. 7 of the Khar'kov Region experiments were made on grazing pigs on an area of 18 hectares in the early spring period (second half of March, April, and the first half of May). These experiments showed that, in the case of non-hybrid varieties, various tuber remnants (tuber halves, eyes, stolons) amounting to 3,000 pieces per hectare were left in the soil; the hybrid tubers, on the other hand, form compact clumps that are wholly consumed by the pigs, no remnants being left. By virtue of their compact tuber clumps, hybrids between sunflower and Jerusalem artichoke are a suitable culture for fodder and field-crop rotations; the difficulty of having to clean the fields, which troubles farmers in rotations with non-hybrid Jerusalem artichokes, does not exist here.

State and collective farms can harvest a high green matter yield from the hybrid varieties in the fall, and can use the tubers in the fall and spring as valuable juicy fodder for all kinds of farm animals, especially pigs. This is of great importance for agricultural production, as there is usually a shortage or a total lack of juicy fodder in the collective and state farms in spring. Besides, if pigs are grazed on plantations of hybrids in early spring, full use is made of the tubers without any expenditure in manpower for harvesting and storing, and hence large quantities of other feeding stuff are saved.

Jerusalem artichoke × sunflower hybrids and the problem of inulin and fructose. Another point to be dealt with is the utilization in the sugar industry of Jerusalem artichoke and its hybrids with sunflower. There are new, not yet widely known possibilities in this matter. A combined enterprise (processing plant and state farm has been established recently at our recommendation in the Tcherkass Region for the production of fructose from hybrid tubers.

Hybrids are a good raw material for the production of fructose. They have a compact clump of tubers, their tubers are large, fan-shaped, have short stolons which do not interfere with cutting during processing, and contain a high percentage of fructose amounting to 22-23% in certain years; the general yield of fructose per hectare is higher than in Jerusalem artichoke (Table 1).

The carbohydrate complex in hybrid tubers that had been stored in clamps during the winter was determined and compared with that of ordinary Jerusalem artichoke (Table 2).

Table 1

TUBER YIELDS, AND CONTENT AND YIELDS OF FRUCTOSE FROM JERUSALEM ARTICHOKE AND ITS HYBRIDS WITH SUNFLOWER, BASED ON EXPERIMENTAL DATA OF THE FORMER INSTITUTE OF GENETICS AND BREEDING, ACADEMY OF SCIENCES OF THE UKRAINIAN SSR (AVERAGE FOR 1953 to 1955)

Variety	Tuber yield (centners/ha)	Fructose content in tubers (%)	Fructose yield (centners/ha)
Jerusalem artichoke Belyi Kievskii	187.0	17.1	32.0
Hybrid between *Jerusalem artichoke* and sunflower, clonal line No. 120	425.1	18.8	80.3

Table 2

CARBOHYDRATE COMPLEX IN TUBERS OF JERUSALEM ARTICHOKE AND ITS HYBRIDS WITH SUNFLOWER (%)

Variety	Monoses	Sucroses	Sugar equivalent of maltose	Starches and hemi-celluloses	Fructoses	Total quantity of sugars	Fructoses in relation to total amount of sugars
Jerusalem artichoke Belyi Kievskii	0.66	3.09	0.69	1.59	10.95	15.35	71.33
Hybrid clone No. 120	0.50	2.48	0.16	1.70	15.61	18.75	83.25

As seen from the above date, the hybrid between Jerusalem artichoke and sunflower has a 3.4% higher content of total sugars and contains 4.66% more basic-carbohydrate fructose than Jerusalem artichoke.

Analyses of hybrid stems made at the biochemical laboratory of the former Institute of Genetics and Breeding of the Academy of Sciences of the Ukrainian SSR and at the carbohydrates laboratory of the Institute of Organic Chemistry of the Academy of Sciences of the Ukrainian SSR* revealed the presence of 12 to 15% of sugars, and in some years of 18% (of the fresh weight).

The stem sugar content can, without a doubt, be increased considerably by breeding, so that hybrids with a twofold utilization by the sugar industry can be developed.

Small-scale production experiments at the Central Sugar Industry Research Institute** have shown that the syrup obtained from stems of hybrids raised by the author at the former Stavropol' Breeding Station has an agreeable taste with a honey flavor. The use of such hybrid species for fructose production is very promising, as additional amounts of fructose (approaching those from the tubers in quantity) can be extracted from the stems.

The susceptibility of Jerusalem artichoke × sun-flower hybrids to diseases, and the possibility of using these hybrids in sunflower breeding. Jerusalem artichoke × sunflower hybrids are marked by a complete immunity to rust and

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broomrape. The problem of combating broomrape on sunflower is almost solved, as is known. Rust control still necessitates much work. None of the presently grown sunflower varieties are unaffected by rust; in some humid districts sunflower cannot be cultivated, because of the seriousness of attacks by this fungus. The raising of rust-immune sunflower varieties is an urgent problem, on which the breeder has to work. According to calculations by the known sunflower breeder V. S. Pustovoit, two million poods* in sunflower oil are lost by each degree of rust affection every year.

Jerusalem artichoke × sunflower hybrids can serve as starting material in the breeding for rust resistance. We studied the progeny of Jerusalem artichoke × sunflower hybrids during seven years and made selections for immunity to rust and broomrape. We found that F_1 hybrids are entirely immune to Puccinia helianthi. In the second and the third generations, segregation into immune and susceptible forms takes place, with a considerable preponderance of the former.

We have done breeding work for rust immunity to the seventh generation, in which there is a vigorous segregation into immune and non-immune families. No cases were observed, where an entire family was immune, but the average degree of affection (in families described as immune) is very low. We have obtained families which are undergoing competitive tests and are being propagated at the Andreev State Farm of the Cherkassy Sugar Beet Trust; they are almost entirely free of rust, give a high seed yield, and surpass the standard varieties in oil yield. Test results of the most productive families are shown in Table 3.

Table 3

MOST PRODUCTIVE FAMILIES OF JERUSALEM ARTICHOKE × SUNFLOWER HYBRIDS OBTAINED IN THE SEVENTH GENERATION

Variety	Seed yield per plot		Husk	Oil	Oil yield per plot		Affection by rust	Thousand-seed weight (in g)
	in g	in %	in %		in g	in %		
Zhdanovskii 8231	1,129	100.0	34.5	54.6	403.7	100.0	1.1	69.1
No. 237	2,060	182.5	41.0	52.0	632.0	156.5	0.3	85.4
No. 230	1,950	172.7	35.2	51.1	645.6	159.9	0.6	71.7
No. 192	1,844	166.8	36.8	51.2	596.6	147.7	0.1	80.4
No. 54	1,672	148.1	37.2	52.0	546.0	135.2	0.3	72.7
No. 72	1,662	147.1	35.0	55.4	598.4	148.2	0.2	72.9

Seventh generation hybrids have also shown a high immunity to broomrape. Families grown in an environment which is favorable for infection were mostly resistant and about 30% of them absolutely immune (Figure 4).

* [A pood (Russian weight) = 36.113 lb.]

FIGURE 4. Third-generation Jerusalem artichoke × sunflower hybrid, which served as starting form in the breeding of rust-immune sunflower

T r i a l p r o d u c t i o n t e s t o f J e r u s a l e m a r t i c h o k e × s u n f l o w e r h y b r i d s. For this test we sent planting material to 30 research institutions, 35 collective farms, and 90 state farms in different zones of the Soviet Union. In addition, hybrids of Jerusalem artichoke with sunflower were tested by many collective farm research workers and young naturalists on school plots.

The trial was made on a wide network stretching from the Far East (Magadan) and to the western Ukraine (Lvov) and from the extreme north (Kandalaksha, Murmansk Region) to the south (Kirovabad).

The following conclusions can be drawn from these tests:

1. In the northern regions (Leningrad, Vologda Regions) and Baltic Republics, the hybrids produced high yields of green matter (800 to 100 centners/ha) and relatively few tubers (150 to 200 centners/ha).

2. In the nonchernozem belt of the European part of the U.S.S.R. there was a lesser yield of green matter (600 to 900 centners/ha) and the same quantity of tubers (150 to 200 centners/ha).

3. In Siberia, the hybrids gave a good yield in the Altai territory. Some state farms of the Altai territory obtained over 450 centners of tubers and up to 600 centners of green matter per hectare.

4. In the arid parts (Kuibishev, Rostov, Kherson Regions), and also in the Azerbaidjan SSR the hybrids gave a good yield when irrigated or when grown in low-lying places. In the Azerbaidjan Animal Breeding Research Institute, 304 centners of tubers and 969 centners of herbage were obtained per hectare with irrigation.

In the Ukraine, the hybrids are grown more successfully; the best tuber and herbage yields are obtained in the more northern and western districts (Chernigov, Sumy Poltava, Kiev, Zhitomir and Vinnitsy Regions); in these districts the tuber yield is between 300 and 400 centners/ha, with a similar yield of green matter.

On the cytology of the Jerusalem artichoke × sunflower hybrids. A cytological study was made of hybrids of the first and second generations, so as to clarify causes of their sterility. These hybrids are also of interest as offspring of parental forms with unequal chromosome numbers (sunflower $2n = 34$, Jerusalem artichoke and wild relatives $2n = 102$).

F_1 hybrids of three combinations with different degrees of fertility were submitted to a cytological study:

1) a highly fertile group - hybrids from the cross between H. annuus and H. macrophyllus;

2) medium fertile group - from the cross between H. subcanescens and H. annuus;

3) weakly fertile, almost sterile group - from the cross between H. tuberosus and H. annuus.

In addition, we are beginning with a study of F_2 backcrosses to clarify the causes of the particularly high sterility in these hybrids. We have to stress that we have made no detailed study of somatic mitosis, but have merely counted chromosome numbers on permanent preparations.

The chromosome count in the somatic cells of F_1 hybrids showed the presence of 68 chromosomes; this is in accordance with hypothetical assumptions (51 chromosomes from Jerusalem artichoke and 17 from sunflower).

We have also made a study of the qualitative composition of pollen grains, in particular of their fertility or abortiveness, of the percentage of normal and degenerated pollen, and of variability in the size of pollen grains.

The species H. tuberosus L. has a high percentage (65.1) of abortive pollen grains. It also has the greatest quantity of degenerated pollen (16.1%) and of pollen deviating in size from the normal (macropollen - 1.7%, and micropollen - 2.2%). It has been proved by Kostoff (1934) that the reduction division in H. tuberosus L. is highly irregular; apparently it is a plant of hybrid origin. There were relatively few abortive pollen grains in the species H. subcanescens (Gray) Wats. (22.3%) and very few in H. macrophyllus Willd. (1.6%).

F_1 hybrids, too, have a high percentage of abortive pollen grains. The highest percentage was observed in the combination H. tuberosus × H. annuus (65.5); it was somewhat lower in hybrids from the cross H. subcanescens × H. annuus (37.2), and the combination H. annuus × H. macrophyllus had the lowest percentage of pollen abortion (6.5). The first two combinations also have a higher percentage of degenerated pollen and pollen deviating from the normal size.

The high percentages of abortive and degenerated pollen, and also of that of pollen of a deviating size indicate an abnormal course of meiosis which generally leads to sterility in the hybrid. The F_1 H. tuberosus × H. annuus hybrids, which have the highest percentage of abortive pollen grains and of pollen of deviating size, have an extremely low fertility and are almost sterile. F_1 H. subcanescens × H. annuus, which have a lesser percentage of abnormal pollen grains, are more fertile than the combination H. tuberosus × H. annuus but less fertile than F_1 hybrids from the cross between H. annuus and H. macrophyllus.

The F_2 hybrids from the backcross of F_1 to sunflower have an even greater variability of pollen grains. In the second generation, high percentages of abortive pollen (80 to 82), degenerated pollen (11.6 to 18.3) and micro- and macropollen (6 to 11) are noted. This is an indication of the exceptional sterility of the hybrids, which has been confirmed by our investigations. Of some thousands of F_2 plants which we have studied, only single individuals produced some few achenes in their flower heads, while all the remaining plants were highly sterile.

While pollen grains of the parental forms are more or less evenly sized, the size of hybrid pollen is very variable, especially in both F_1 and F_2 sterile groups. This is particularly apparent in the F_1 combinations H. tuberosus × H. annuus, F_1 H. annus × H. tuberosus, F_1 H. macrophyllus × H. annus, and the F_2 and F_3 hybrids.

In the fertile group of first-generation hybrids (H. annuus × H. macrophyllus) the formation of 34 bivalents was observed as well as a complete absence of univalent chromosomes. It has been established that there is a complete autosyndesis of chromosomes of species H. macrophyllus Willd. in these hybrids.

In the group of partially fertile hybrids (H. subcanescens × H. annuus), the reduction division is somewhat disturbed as a result of three univalents failing to become included in the nucleus. During diakinesis the presence of univalents and bivalents together with other configurations (trivalents and multivalents) has been observed. In most cells there were one, and sometimes two or three univalents, which generally isolated themselves and formed micro-pollen grains.

The presence of three univalents in hybrids between sunflower and H. subcanescens (Gray) Wats. indicates that the basic haploid chromosome number of the species H. subcanescens (Gray) Wats. cannot be 17, but is 16 plus an odd chromosome which has its individual behavior in crosses. There is no full autosyndesis, as observed in the cross of the sunflower with H. macrophyllus Willd. in this combination, but a partial one, leading to an incomplete fertility of hybrids (I. I. Marchenko, 1947).

We have not completed our investigations of the group of sterile hybrids H. tuberosus × H. annus. From the preliminary study of pollen mother cells it is seen that the reduction division in these hybrids is markedly disturbed, with a large number of chromosomes failing to become included in the nucleus and with the formation of triads and even diads together with normal tetrads.

The genus Helianthus L. is one of the largest genera of the family Compositae. It numbers more than 100 species, which are of considerable interest for breeding. The majority of wild-growing species are not affected by rust, broomrape and other diseases of our cultivated sunflower. Many species of this genus grow on solonets and solonchak, on desert, stony and sandy soils, and withstand severe climatic and edaphic conditions. Tuberous and even nontuberous species are of interest for the improvement of Jerusalem artichoke, which has a fodder and industrial importance. By utilizing annual and perennial species of the genus Helianthus in hybridization, varieties of Jerusalem artichoke with a heightened content of inulin in the tubers can be developed, the tuber shape can be improved, the clump of tubers can be made more compact, and this plant can be rendered suitable for use in fodder and field-crop rotations.

Work in interspecific hybridization in the genus Helianthus has been done by only a few scientists (Cockarell, Thellung, Wagner, and others) on limited material of no practical value. Work with a practical application has only been carried out in the U.S.S.R. during the last decade. Hybridization has been done with a view to improving the basic oil crop - sunflower (Satsyperov, Plachek, Pustovoit), and also Jerusalem artichoke (Shibrya, Marchenko, Davidovich).

The first hybrid generation obtained by us is marked by a high variability in all morphological-physiological characters, such as length of the vegetative period, tuber-forming ability, branching characters, leaf shape, stem pigmentation, etc.

The fertility of the first-generation hybrids depends on the parental pairs taken for the cross. The first generation from the cross between cultivated Jerusalem artichoke (H. tuberosus L.) and sunflower proved to be almost sterile; a group of hybrids of medium fertility was obtained from crosses of sunflower with the wild relative of Jerusalem artichoke - H. subcanescens (Gray) Wats.; highly fertile hybrids resulted from the cross of sunflower with another wild relative of Jerusalem artichoke - H. macrophyllus Willd., especially if sunflower was taken as seed parent. In the second generation, a complete sterility of the hybrids was observed in all cases.

The hybrids between Jerusalem artichoke and sunflower are characterized by a complete immunity to rust and broom rape and also to other diseases, with the exception of sclerotinia. The hybrids served as our starting forms in sunflower breeding. In the F_7, families having an entire or almost entire immunity to these diseases were obtained; these families also surpassed such standard varieties of sunflower as Zhdanovskii 8281, VNIIMK* 6540, and others in seed yield, thousand-seed weight, and oil yield.

The majority of first-generation hybrids are considerably more vigorous in their development of green matter than the starting forms. In tuber-forming ability, Jerusalem artichoke characters dominate in first-generation hybrids; the tuber yield varies between 100 to 200 g to 4 kg per plant. There are a few segregants with an annual life cycle.

Hybrids between Jerusalem artichoke and sunflower which have been obtained and introduced in the collective and state farms of the Ukrainian SSR and other republics of the Soviet Union belong to two hybrid clonal lines - No. 15 and No. 120. Both these clones are intermediate between

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Jerusalem artichoke and sunflower in their external characters. They give high yields of tubers and green matter valuable for silage; this is owing to their pronounced heterosis which is fixed by vegetative propagation.

In the forest-steppe zone of the Ukrainian SSR, clonal line No. 120 yields 30 to 40 tons of tubers and 60 to 70 tons of green matter per hectare under favorable conditions. The hybrid No. 15 yields 15 to 18 tons of tubers and 75 to 80 tons of green matter per hectare. These green-matter yields are one-and-a-half times to twice as high as those from ordinary varieties of Jerusalem artichoke.

The hybrids between Jerusalem artichoke and sunflower also possess very good qualities as fodder plants: their green matter contains up to 12% of sugars and up to 3% (of the fresh weight) of digestible protein; the hybrids are on a level with corn in fodder value and are superior to sunflower grown for silage. The nutritional value of the hybrid tubers is much higher than that of such crops as fodder beet, fodder carrot, or swede.

Hybrid clonal line No. 15, which produces high yields of tender green mass and has a somewhat lower tuber yield, is being introduced by us to large meat-milk stockbreeding farms, where greens rather than tubers are required. Clonal line No. 120, the asset of which lies in its tuber yield, is being introduced mainly in pig-breeding farms and pig farms of the collective farms.

Hybrid clone No. 120 has a compact clump of tubers; it can be lifted from the soil easily, without any small tubers being left behind. This property makes line No. 120 a suitable culture for field and fodder-crop rotations without any necessity for the fields to be weeded.

Jerusalem-artichoke × sunflower hybrids have high contents of inulin in their tubers (20 to 22%) and may be of interest as a new industrial crop for fructose production. Crystaline fructose obtained by laboratory and semi-industrial methods at the Institute of Organic Chemistry of the Academy of Sciences of the Ukrainian SSR is of interest for the cake industry and medicine. In view of this desirable raw material, a combined fructose-producing enterprise has been set up in the Cherkassy Region.

In stems of the hybrids, 12 to 15% of total sugars have been found, so that these plants may possibly find use in the sugar industry together with cane sugar.

The hybrids between Jerusalem artichoke and sunflower have passed production tests in recent years in 200 collective and state farms and have also been investigated by collective farm research workers in different parts of the Soviet Union. On the whole they have shown themselves commendable.

RESULTS OF WIDE HYBRIDIZATION IN BEET

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Summary of Report

As a result of expeditions in which wild beet species were found and collected, many valuable morphological and physiological properties were determined in these species (one-seededness of the fruit, winter hardiness and cold resistance, drought resistance, salt tolerance, resistance to Cercospora beticola, curly top, yellows virus and nematodes). The desirable properties of wild beet species can only be utilized with the aid of wide hybridization between the former and cultivated beet, as wild species have negative traits together with positive ones.

Hybridization between species of the section Patellares and cultivated beet is in its very beginning, and hybrids are only obtained with great difficulty, despite the large scale on which crosses are made.

According to the data of certain investigators, wide hybrids between cultivated beet and wild species of the section Vulgares, e. g., species Beta Webbiana Moq., B. procumbens Chr. Sm., and B. patellaris Moq. are inviable; the reason is that no secondary thickening takes place in the roots of the hybrid seedlings.

The first experiments in grafting first-generation hybrids on sugar beet indicate a possible way of maintaining the seedlings alive. In single interspecific hybrid plants of the cross B. vulgaris × B. patellares which reached the flowering stage, both pollen and ovule are defective, the latter rapidly becoming necrotic.

According to other data, B. vulgaris × B. procumbens hybrids were maintained up to the third generation in spite of difficulties. This points to the importance in wide hybridization of differences in the starting material and in ecological conditions.

Our investigations in interspecific hybridization with members of section Corollinae have proved that the perennial hexaploid species B. trigina W. et K. (2n = 54) is a natural interspecific hybrid of the amphidiploid type. Plants of the species B. trigina (2n = 54) are marked by an

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intermediate complex of morphological and physiological characters, typical for this hybrid's parental species - B. lomatogona F. et M. (2n = 18) and B. corolliflora Zoss. (2n = 36).

The autotetraploid species B. corolliflora (2n =36) which we obtained possesses a strong stem, strong roots and the largest flowers.

The species B. intermedia Bge. originated apparently from the cross between B. trigina (n = 27) and B. lomatogona (n = 9) and is also characterized by an intermediate type of inheritance of the parental species' characters.

The one-seededness of the fruit of B. lomatogona is a recessive character in crosses with other species possessing many-seeded aggregate fruit, and the number of seeds in the fruit of first-generation hybrids varies between 1 and 2 or 3. The degree of fertility of first-generation plants is variable. This indicates the need for effective methods of obtaining first-generation hybrids.

The hybrids of sugar, beet, mangel, and table beet with such wild species of the section Corollinae as B. macrorrhiza Stev., B. lomatogona, B. corolliflora, and B. trigina are obtained with difficulty and are sterile in the F1. In the first generation, interspecific hybrids exhibit heterosis and variability in the dimensions, number, shape and weight of the leaves. The inheritance of the morphological and physiological characters of the first generation are largely intermediate between those of the parent species, with deviations to the side of the wild parent species. As a consequence of increased growth and modifications of the morphological and physiological make-up of the roots, interspecific hybrids exhibit the cold-resistance characters of the wild parent species to a considerably lesser degree.

In triploid (2n = 27) interspecific B. corolliflora × B. vulgaris hybrids the chromosome complements of both parent species can be clearly distinguished, owing to the different sizes of these complements.

Irregularities of reduction division vary in different first-generation plants, and there is a large variability in the degree of sterility or fertility in the backcrosses which are made with the aim of obtaining seed from first-generation hybrids. This indicates that considerable numbers of first-generation hybrid plants are essential for successful work.

The B. lomatogona character of one-seededness of the fruit is recessive in crosses with many-seeded cultivated beet, and the seed number in fruit and fruit aggregates of the first generation is intermediate. In such crosses, as well as in intercrosses between [B. lomatogona and] wild species, vegetative characters segregate already in the first generation.

Methods of establishing preliminary vegetative contact between poorly crossing Beta species by grafting and subsequent backcrossing to the stock species are most promising and may help to make work on wide hybridization in beet easier. The stocks and scions used can be of one age or - which seems even better - of different ages.

Differences between species of section Vulgares are less considerable than those between species of other sections, so that interspecific hybridization within this section is easily accomplished.

First-generation hybrids from crosses between B. maritima L. and cultivated beet exhibit heterosis which manifests itself in increased size, and number and weight of the leaves. In some morphological-physiological characters the hybrids are intermediate between their parents, with a greater or lesser deviation to the side of the wild species. In the first generation, a segregation of color characters of the root is observed. The yellow pigments are correlated with the increased weight of the root and a lowered sugar content, while red pigments (anthocyanins) are associated with lower root weight and higher sugar content.

The inheritance of sugar content in first-generation hybrids between B. maritima and leaf beet or sugar beet is intermediate in type, and in hybrids with mangel the complex of wild-beet characters determining sugar accumulation is almost dominant. An intermediate type of inheritance with a deviation to the side of the wild species has been established with regard to resistance to Cercospora beticola. The phylogenetic proximity between B. maritima, leaf beet (B. maritima ssp. cicla), and sugar beet is borne out by a complex of characters promoting intensive sugar accumulation, which stands in contrast to a limited sugar accumulation in mangel and table beet.

Our theory that sugar beet is of hybrid origin and that it is derived from remote ecological-geographical crosses between leaf beet and mangel with a subsequent improvement of the hybrids through special agricultural measures and selection for increased sugar content, has been confirmed.

Our experiments also confirmed the great practical significance of diallel crosses, through which the hybridization value of the crossed parental pair can be determined very precisely in the first generation.

Comparative studies of wide hybrids of the second, third and fourth generations, obtained by various methods, have demonstrated the outstanding value of the method of backcrossing the best selected first-generation hybrid plants to varieties of sugar beet. As in hybrids of cultivated beet, backcrossing eliminates the negative phenomena of near-relative multiplication and leads to the production of highly productive wide hybrids in the second, third and fourth generations.

Under favorable growing conditions, the best third-generation hybrids derived from backcrosses of the first generation to parental forms of sugar beet surpassed the standard variety of sugar beet in harvests and sugar output by 20 to 30%.

Wide hybrids of the third and fourth generations have a very negative reaction to air and soil drought accompanied by high temperature. It has been found that B. maritima × sugar-beet hybrids are a moisture-loving, late-ripening leafy type of beet, and may show themselves suitable for humid destricts with a moderate temperature regime.

Third-generation hybrids from a single backcross of the first generation to sugar beet are more resistant to Cercospora beticola than hybrids from two backcrosses.

During the post-war period, work on wide hybridization in beet was severely reduced. From 1944 to 1948, when no new backcrosses were carried out in fifth, sixth and seventh generations, the index ratings of economic qualities in B. maritima × sugar beet hybrids, recorded in elite and superelite selections, deteriorated. It has been proved experimentally that this was the result of near-relative multiplication and accumulation of quick-ripening low-sugar forms which are best adapted to our soil and climatic conditions.

By now, considerably improved eighth-and ninth-generation hybrids have been obtained through backcrossing and, particularly, biological selection. These forms are not inferior to the best production varieties of sugar beet.

With the development of beet cultivation for industrial purposes in western humid districts of the Ukraine, Belorussia, and Lithuania, work on wide hybridization between wild and cultivated beet will have to be expanded considerably.

WIDE HYBRIDIZATION IN THE GENUS LYCOPERSICON TOURN.

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On a basis of studies of the entire range of forms within the genus Lycopersicon Tourn., the senior author has separated three species: a) L. peruvianum (L.) Mill., b) L. hirsutum Humb and Bonp., c) L. esculentum Mill., which are differentiated by definite morphological and biological characters.

The species L. glandulosum established by Mueller (1940) shares so many traits with L. hirsutum that it seems expedient to consider it as a variety of species L. hirsutum; certain - basically quantitative - differences cannot serve as a sufficient basis for considering L. glandulosum an independent species. The species Cheesemanii has been separated from the polymorphic species L. peruvianum by Riley (1925). According to the system of Mueller (1940), L. Cheesemanii belongs to subgenus Eriopersicon. The distinguishing characters of tomatoes of this subgenus are pubescent ovaries and fruit, and almost naked seed; the color of the fruit is white, greenish-white, sometimes yellowish. L. Cheesemanii is endemic on the Galapagos Islands and, according to recent investigations (Rick, 1956), its affiliation to the subgenus Eriopersicon is doubtful. From Mueller's description L. Cheesemanii can only be a variety of L. peruvianum. Thus, among wild forms only two can be definitely considered species: L. hirsutum and L. peruvianum.

At the All-Union Institute of Plant Cultivation, wide hybridization was carried out between L. esculentum and the wild species L. hirsutum and L. peruvianum. Crosses involving the same species were made at the Gribov Vegetable Breeding Experimental Station. In work at the Main Botanic Gardens of the Academy of Sciences of the U.S.S.R. representatives of genera, other than Lycopersicon were also involved in crosses with tomato.

Cytological studies of interspecific tomato hybrids are under way at the Institute of Genetics of the Academy of Sciences of the U.S.S.R. The species L. peruvianum is very polymorphic; plants of this species have a decumbent habit, their stems are thin with a pubescence consisting of appressed hairs; leaves and fruit have the same pubescence; the inflorescence is a furcate raceme, the flowers are yellow, the anthers closely united in a narrow column, the pistil is filiform with a small stigma scarcely protruding - or protruding somewhat more - above the staminal column. The fruit are spherical with dorsally concave seed, two-celled, of a diameter of 1 to 2 cm, with red-violet vertical lines or a flush of a similar color.

The fruit of L. peruvianum contain a higher percentage of dry matter (12.75) and vitamin C (50 mg% and more) than those of other species.

Early studies of L. peruvianum in the U.S.S.R. as well as abroad showed that plants of this species are non-susceptible to tobacco mosaic, leaf mold, Septoria, Fusarium wilt, Alternaria bacterial spot (Xanthomonas vesicatoria), and nematodes. Some forms of L. peruvianum proved to be resistant to Phytophthora.

Plants of the species L. hirsutum have thick, brittle stems, densely covered with long, erect hairs and a large number of glandular hairs. L. hirsutum plants have a specific strong odor, differing from that of ordinary tomato. The leaves are large, light green or green, the segments entire, dentate at margins. The inflorescence is a simple or furcate raceme. The flowers are brilliant yellow, the corolla is weakly split, the staminal column is somewhat thicker than in L. peruvianum, but narrower than in L. esculentum, the pistil is thin, the stigma small and protrudes from the column in the form of a lobed small stigma. The fruit are small, 1 to 2.5 cm in diameter, spherical, sometimes slightly flattened or elongate, two-celled, densely covered with long hairs, green or whitish, sometimes with a few brown-violet lines.

In the collection of the All-Union Institute of Plant Cultivation, the species L. hirsutum is represented by only one specimen, so that we are not in a position at present to judge the range of forms within this species, though it is clear from the literature that numerous varieties exist within this species too. Mueller separates the form glabratum in particular, which is marked by a less dense stem pubescence and by appressed and not erect hairs on the leaf, long ciliate hairs at the margins of the segments, and a flower which is somewhat smaller than in L. hirsutum.

The species L. hirsutum possesses a high resistance to Alternaria, Septoria, leaf mold, certain strains of Fusarium, tobacco mosaic, and, apparently, to Phytophthora. It is not resistant to nematode damage.

It is noteworthy that the material of the given species available to us was markedly lacking in uniformity both morphologically and in biological characters.

The first crosses of ordinary tomato with L. peruvianum were effected in 1933, 1934 and 1935 in the Kamennaya Step' Experimental Breeding Station of Voronezh Region; some tiny seeds were obtained, of which only one germinated. The hybrid plant had an intermediate structure with a dominance of paternal L. peruvianum characters. There were irregularities in the processes of pollen formation (univalents, laggard chromosomes, etc); a subsequent project on wide hybridization of tomato at the experimental station was interrupted. In 1950, work on wide hybridization of tomato was begun in the All-Union Institute of Plant Cultivation near Leningrad, on the trial grounds of the Pushkin Laboratories of the same institute and at Leningrad State University (Staryi Petergof). Our aims included: 1) the working out of methods which would counteract incompatibility between plants of cultivated tomato and the species L. peruvianum and L. hirsutum, b) counteracting sterility in the hybrid generations, c) finding ways to obtain constant forms with economically desirable characters.

The method of working with a preliminary intermediary was used by the Vegetable Crops Division of the All-Union Institute of Plant Cultivation in 1950 and 1951, in conjunction with work done at Pushkin (K. V. Ivanova): seed-parent plants of species L. esculentum were grafted in the cotyledon stage onto more developed plants of L. peruvianum and L. hirsutum (five-to-six true-leaf stage). Wild tomatoes served as pollen parents. Pollen of the species constituting the stock of the graft was placed several times on the stigma of the emasculated flower. Different pollination methods were used in 1952 to 1954 (T. B. Batygina): single, double and triple pollination with the pollen of only one wild species; multiple pollination with various mixtures of pollen*; pollination with the column of anthers, or with part of the (paternal) gynaecium attached.

With the aid of these methods, normally developed seed was obtained in a sufficient quantity for observations on the inheritance and segregation of parental characters in the progeny.

It is noteworthy that the percentage of fruit set in tomato, following the use of different methods of pollination, gives no indication of the number of seeds that will develop, as quite a percentage of parthenocarpic fruit are formed. In crosses between L. esculentum and L. peruvianum, for instance, 56% of fruit set in three years, comprising only 10.9% which contained seed.

Methods of multiple pollination with pollen of one species and with a pollen mixture proved most effective; by these methods, a large number of pollinated fruit is obtained, as well as a sufficiently fertile progeny. Success depends not only on the method of pollination, but also on the choice of the seed-parent variety. From crosses with variety Shtambovyi karlik [Shtambov Midget], for example, larger numbers of seed developed than from others with variety Fikaratstsi as seed parent.

In interspecific hybridization of tomato it often happens that seed is formed which cannot conclude its cycle of development; under certain conditions the embryo is absent in them, in other cases the seed coat. Underdeveloped hybrid embryos can be raised successfully on a special nutrient medium.

* Added pollen comprised that of the second wild tomato species, of the seed parent (L. esculentum), nightshade [Solanum nigrum?], Physalis, or wild potato.

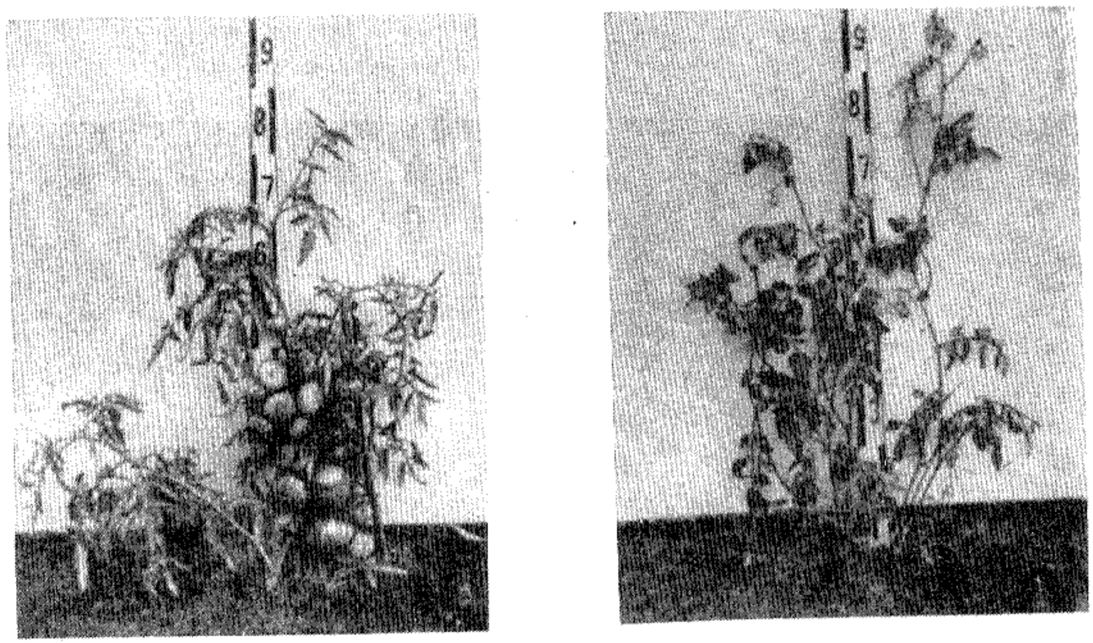

FIGURE 1. Parent species. Left–*Lycopersicon esculentum*, variety Taezhnik; right–*L. Peruviarum*

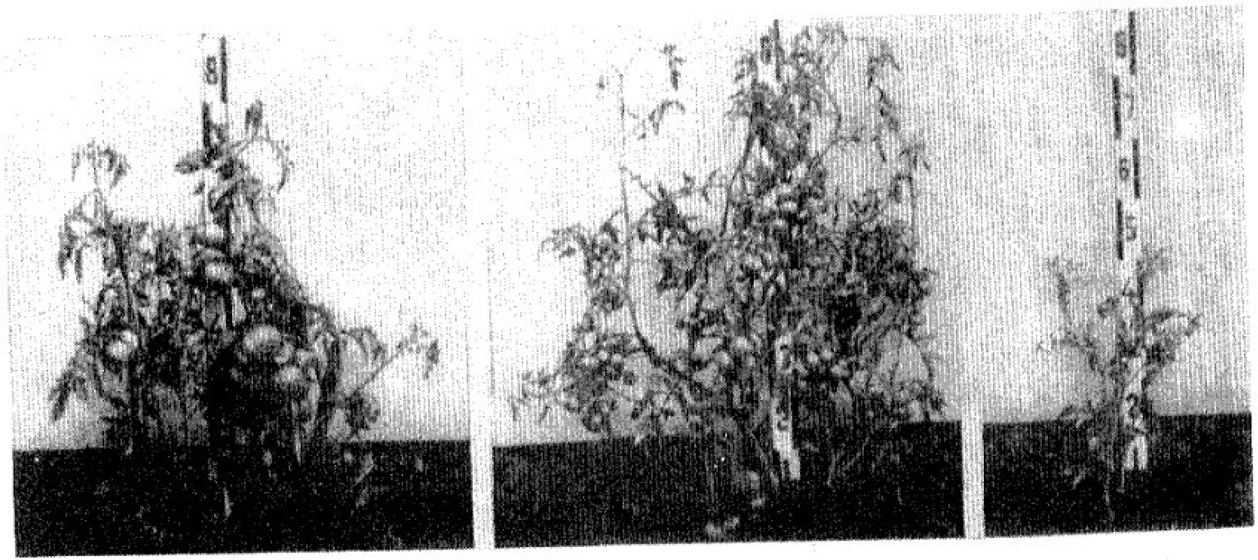

FIGURE 2. Hybrid forms of *Lycopersicon esculentum* × *L. peruvianum*

From left to right: *esculentum* type, intermediate type, *peruvianum* type.

Hybrids between L. esculentum and L. peruvianum. First-generation plants resulting from the cross between ordinary tomato and L. peruvianum are mainly - and often wholly - of the seed-parent L. esculentum type. This inheritance of the seed-parent type often throws doubt on the hybrid nature of the progeny, and the possibility of the emasculated flower having become fertilized by its own pollen has to be taken into account; in anatomical characters, F_1 plants are often intermediate. Segregation is sometimes observed in F_2 and F_3, but the L. esculentum type always remains dominant. In one of the F_1 combinations, there were five plants of the pollen-parent type, but all of them proved to be sterile.

When methods of pollinating two or three times and pollination with a pollen mixture of L. peruvianum and the maternal variety were used, quite a number of plants of the intermediate type were obtained (Figure 2). In subsequent generations these intermediate forms continued to appear; intermediate forms comprised plants the fruit of which were yellow, red and orange when ripening and had two to six small locules. Variability in size and color of the fruit could be observed even within the same plant.

In rare cases, new forms appeared from crosses between L. esculentum and L. peruvianum. Such a new form resembling the currant-tomato (L. pimpinellifolium), but not altogether identical with it, has been obtained at Pushkin; during a number of years, no segregation whatsoever was observed in this form (Figure 3).

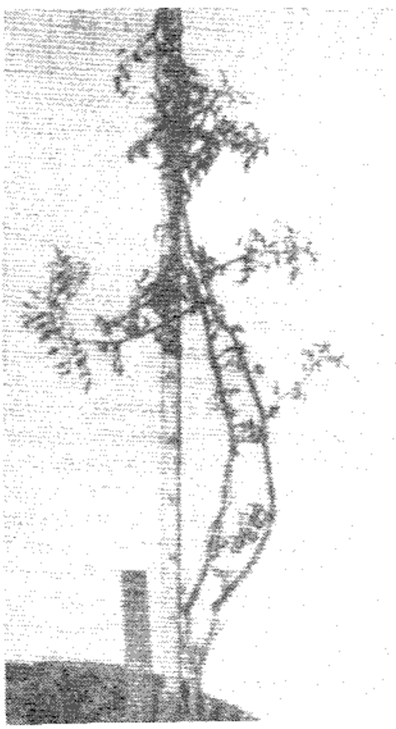

FIGURE 3. Lycopersicon esculentum × L. peruvianum - constant form of the currant-tomato type

Hybrid material derived from the cross between L. esculentum and wild species was submitted to field trials on resistance to septoris and macrosporium at the Maikop Experimental Station of the All-Union Institute of Plant Cultivation (Voskanyan).

In the combination of variety Taezhnik with L. peruvianum there was a somewhat increased resistance in F_1 (as compared to the cultivated parent), but this resistance dropped in subsequent generations. In plants of the intermediate type, resistance was maintained somewhat longer. The rapid loss of resistance can be explained by the fact that no preliminary choice of the resistant parent forms of the wild species was made; pollen was collected from flowers of the undivided population of L. peruvianum.

L. hirsutum hybrids. Crosses between L. esculentum and L. hirsutum are accomplished more easily than those involving L. peruvianum; quite often fruits with a large number of seed are obtained. One single pollination of cultivated tomato with pollen of L. hirsutum, however, results in the formation of seed only in exceptional cases. Results of crosses between these species are summed up in the following:

NUMBER OF FRUIT CONTAINING SEED (%) OBTAINED BY CROSSING L. ESCULENTUM WITH L. PERUVIANUM AND L. HIRSUTUM (DOUBLE AND TRIPLE POLLINATION)

Years	L. esculentum × × L. peruvianum	L. esculentum × × L. hirsutum
1952	22-25	85
1953	1.9-6.6	65-70
1954	14-24	50-84

The analysis of first-generation hybrids obtained from crosses between cultivated tomato and L. hirsutum shows a dominance of the pollen-parent type in that generation: F_1 plants flower earlier than L. hirsutum plants, fruit set in many of them, but, as in the seed parent, only under short-day conditions; isolated fruit set on the first inflorescences, and some fully developed seeds were formed in them. Completely ripe F_1 fruit are yellow in color. Very rarely, usually when a pollen mixture is used, forms of the seed-parent and intermediate types appear in the first generation. In the second and third generations, the pollen-parent type still predominates, and forms of intermediate and seed-parent types continue to segregate in hybrids obtained from pollination by a pollen mixture.

In some forms, L. hirsutum characters dominate, in others L. esculentum characters. Many plants are of limited growth; the leaf segments are subdivided to various degrees, and pubescence on the whole plant and on the fruit is from dense to very sparse. The coloring of the ripe fruit is variable: from light yellow to red and red-brown. The fruit are of various shapes and weight - from 1.5 or 2 g to 35 or 40 g. Seed content of the fruit is variable.

Trials of resistance to macrosporium and septoria show a high resistance in hybrid forms deviating in the direction of L. hirsutum.

FIGURE 4. Parent forms; left - Lypersicon esculentum, variety Shtambovyi karlik; right - L. hirsutum

Backcrosses (B) to cultivated tomato provoke marked heterosis and result in a large diversity of forms in B_1, among them plants which bear fruit even on a long day. L. hirsutum and its hybrids do not produce fruit under the northern long-day conditions (Pushkin near Leningrad); work with them can only be done with the aid of special (dark) chambers. The necessity of an artificially shortened day is dispensed with already in the first backcrosses. However, there are still many sterile plants in the B_1. Seed-parent characters are clearly exhibited in leaves, inflorescences, and flowers; there are considerably fewer plants with L. hirsutum characters, which are, as a rule, poorly developed, of reduced height, thin-stemmed, with small leaf segments, and often with an undeveloped inflorescence. In the second and third backcross, a large majority of cultivated plants may be obtained. These are often earlier ripening than the early parent. The fruit have a good taste, are smooth, red, and weigh 40 to 100 g. Segregation continues in some few families even after the third backcross, but, in the majority of cases, selection for economically desirable characters is already entirely possible.

As a result of the investigations, the conclusion can be drawn that the wild tomatoes L. peruvianum and L. hirsutum are not the most convenient objects for breeding work, but there are means for overcoming incompatibility: the sterility of hybrids of the first generation can be overcome through backcrosses and pollination with a pollen mixture. These methods contribute also to the increase of form variability already in the F_1, which enlarges possibilities of selection. The obtaining of economically valuable, higher yielding, and earlier forms with an increased content of dry matter and Vitamin C is entirely feasible.

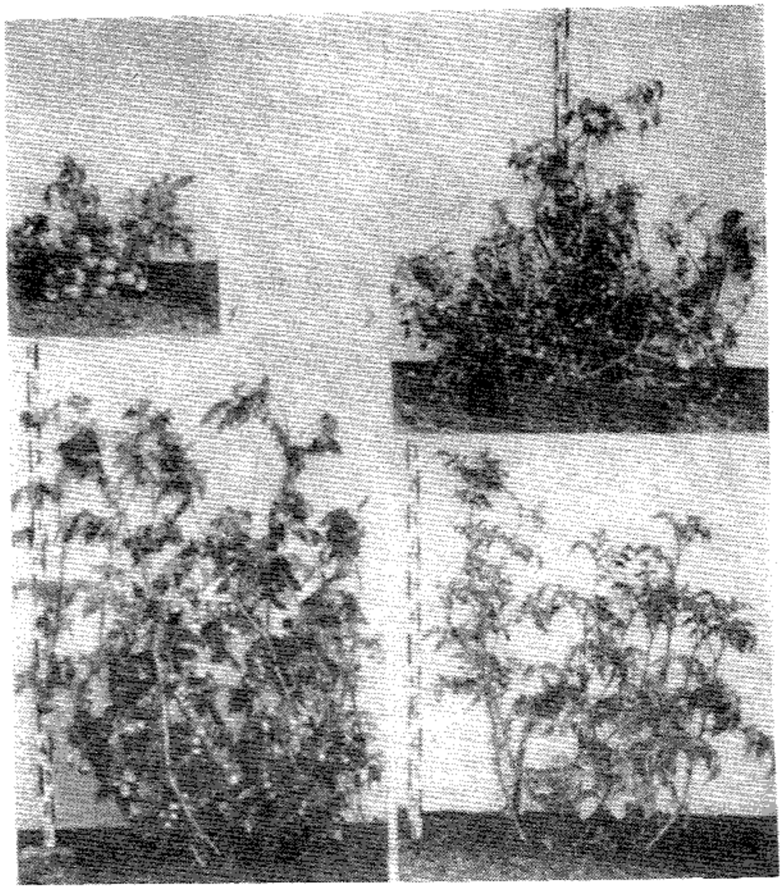

FIGURE 5. Hybrid from L. esculentum × L. hirsutum; 1 - esculentum type; 2 and 3 - intermediate forms; 4 - hirsutum type.

A much more difficult task is the maintaining of F_1 resistance to diseases in advanced generations. The choice of the seed-parent variety and the utilization of wild tomato lines and clones, whose resistance has been checked as pollen parents, will be decisive in this task.

INTERSPECIFIC HYBRIDIZATION OF WATERMELONS

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The variety composition in the U.S.S.R. of table watermelons is far from ideal. Many varieties have excellent qualities together with a number of substantial shortcomings: a poor keeping quality, often unsatisfactory transport qualities, susceptibility to a number of diseases, an insufficient drought resistance, etc.

Interspecific hybridization, with the aid of which shortcomings of the existing watermelon varieties can be eliminated and entirely new economically important types can be synthesized, is imperative for a radical improvement of the assortment of table watermelons now in use.

We worked on hybridization of watermelon species for several years at the Central Asian Experimental Station of the All-Union Institute of Plant Cultivation (Tashkent). Our work was interrupted and then resumed at the Moldavian Research Institute or Irrigated Agriculture and Vegetable Cultivation (Tiraspol').

Three main watermelon species were investigated: Citrullus edulis Pang., C. colocynthoides Pang., and C. colocynthis (L.) Schr.

In the following we give a brief description of the mentioned species. Citrullus edulis is a table watermelon with a juicy, sweet fruit pulp; it is well known, widely cultivated, and was introduced into cultivation long ago. C. colocynthoides is a fodder watermelon with a compact unsweet pulp, which is only in the early stages of being cultivated. If the history of the introduction of table watermelon to the territory of Old Russia has been lost through the many centuries which have passed, the history of fodder watermelon belongs to our time and counts no more than three decades. The fodder watermelon is interesting for hybridization because of the following: 1) a good keeping quality of the fruit; its fruit can be kept for one, two, and even three years, due to a high content of pectins (from 10 to 19% of the dry weight); 2) large fruit and high yields; the fruit reach a weight

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of 15 to 20 kg, and the yield amounts to 500 - 800 centners/ha, which is twice or three times the normal yield from table watermelons; 3) immunity to a number of diseases and lesser demands on cultivation conditions. But, together with these mentioned qualities, there are also certain shortcomings: a fairly late ripening and a fruit pulp which is not sweet and is too compact.

Citrullus colocynthis is a wild plant with a white, bitter, poisonous pulp. It is characterized by a wide area of distribution, thanks to its exceptional adaptability to the severe conditions of waterless deserts. The colocynth has a larger number of traits which are significant for breeding purposes than fodder watermelon, namely: 1) an outstanding, unique drought resistance; 2) many-fruitedness; 20 or even 30 fruit are produced on one plant, whereas in other watermelon species no more than two to five fruits are produced; 3) the fruit may be stored for long periods; 4) short, trailing stems; the vines of the colocynth are approximately half the length of those of table watermelon; 5) immunity to many diseases.

The following negative characters are inherent in colocynth: bitterness and toxicity of the fruit pulp, the small size of the fruit (100 to 400 g) and fairly late ripening, later even than in fodder watermelon C. colocynthoides.

It is seen from the above that the species C. colocynthoides and C. colynthis possess a number of valuable characters which are absent in C. edulis. This warrants their promising use in hybridization with varieties of table watermelon.

Direct and backcrosses between the three described species were carried out by us, with the use of a few forms and varieties of each species.

The percentage of success in intercrosses between watermelons varies between 3 and 31. There is a markedly lowered number of seeds in the hybrid fruit, i. e., there are sometimes 4 to 40 seeds per fruit instead of the normal 400 to 600. Hybrid seed is often of a poor shape, underdeveloped, or has an entirely normal external appearance but germinates badly. This is illustrated by Table 1.

Table 1

RESULTS OF CROSSES BETWEEN WATERMELON SPECIES

Crossed species	Crossability (%)	Seed in hybrids (% of normal seed number)	Germination of hybrid seed (%)
C. edulis × C. colocynthoides	31	23–44	57
C. colocynthoides × C. edulis	13	44–52	54–95
C. edulis × C. colocynthis	3	22–31	62
C. colocynthis × C. edulis	22	5–4	35
C. colocynthis × C. colocynthoides	18	1,5–11,5	–
C. colocynthoides × C. colocynthis	7	–	–

The table shows that in reciprocal crosses of the same species combination, crossability, seed set, and viability of the seed are apt to differ. The first-hybrid generation C. e d u l i s × C. c o l o c y n t h o i d e s is marked by a dominance of C. c o l o c y n t h o i d e s characters and also by a distinct heterosis of the vines, leaves, and size and weight of the fruit (Table 2).

Table 2

HETEROSIS IN LENGTH OF THE TRAILING PLANT AND WEIGHT OF THE FRUIT OF F_1 HYBRIDS BETWEEN TABLE WATERMELON AND FODDER WATERMELON

Indices	Table watermelon variety Belyi dlinnyi [White Long]	Fodder watermelon	First Generation
Weight of the fruit (kg)	3–4	7–80	15–25
Length of stem (m)	2–4	3–5	7–10

The second generation does not exhibit much variability; most of the forms essentially approach C. c o l o c y n t h o i d e s in all characters, i. e. they are late-ripening and have a coarse compact unsweet fruit pulp and a thick peel. Forms, in which the specific characters of C. e d u l i s dominate, constitute only 1 to 3% of the entire composition of the second generation. In order to increase the number of forms of the e d u l i s type, backcrosses to table watermelon varieties have to be made already in the first generation. The heterosis phenomenon, which is observed in the first generation, disappears in the second generation.

In evaluating the group of C. e d u l i s × C. c o l o n c y n t h o i d e s hybrids from a breeding point of view, one is bound to note the great practical significance of such crosses. In the first place, forms with a less compact, less coarse pulp and with a greater sugar content can be obtained, i. e., forms of an improved fodder type. At present, some breeders work in this direction to improve fodder watermelon. Secondly, small numbers of plants are obtained which approach table watermelon in the sugar content of their fruit, but whose fruit pulp is more compact than that of C. e d u l i s; this is a most valuable feature in transport and storage qualities. As has already been said, the compactness of the pulp derives from the high pectin content of the fruit inherent in C. c o l o c y n t h o i d e s.

In the following we give data on the segregation of sugar and pectin content characters in table × fodder watermelon hybrids (Table 3).

Table 3

SEGREGATION OF SUGAR AND PECTIN CONTENT CHARACTERS IN HYBRIDS BETWEEN TABLE AND FODDER WATERMELON (ACCORDING TO DATA OF V.V. ARASIMOVICH)

Parents	Total sugars (%)	Pectins (% of dry weight)
(variety Tsukatnyi [Candied])	2.24	10.87
(variety Kleklei)	9.35	0.91
	5.69	3.56
	5.71	1.44
	1.52	6.50
	6.11	4.23
	3.50	6.30
	4.55	1.63
	5.22	1.92
F_2 plants	5.21	3.26
	5.31	1.86
	6.03	3.30
	5.49	–
	5.43	2.10
	5.19	1.45
	6.01	6.93
	6.13	0.63

Owing to the considerable immunity of fodder watermelons, forms of the table type which are immune to diseases can be obtained through hybridization of C. edulis with C. colocynthoides. Almost all the modern breeding of watermelons for immunity in the U.S.A. is based on hybridization of water watermelons with fodder ones.

Quite recently a new variety of table watermelon, which is resistant to fusarium wilt, has been produced in the Soviet Union at the Bykov Melon Production Experimental Station. It must be noted, however, that the development of new varieties of table watermelon through hybridization with fodder types involves prolonged selection and measures to induce homozygosity, with the obligatory use, as has already been said, of a backcross to C. edulis. The production of improved varieties of fodder watermelon is less laborious and can be accomplished within a shorter time.

Hybrids of C. edulis × C. colocynthis. The first generation of these hybrids exhibits an almost complete dominance of C. colocynthis characters. First-generation plants are late-ripening colocynth forms with a bitter pulp, though with somewhat enlarged fruit and leaves. It is noteworthy that, in crosses between C. edulis and C. colocynthis as in crosses with C. colocynthoides, the length of the vegetative period depends to a considerable degree on the respective reciprocal crosses (Table 4).

The particular characteristic of F_1 hybrids between table watermelon and colocynth is the pronounced heterosis in the length of the vines; the main stem of the colocynth is on an average 1 to 2 m in length, that of the table watermelon - 2 to 4 m, and that of F_1 hybrids – 10 to 12 m.

The second generation differs only slightly from the first; colocynth characters dominate in the segregation, but some forms manifest an influence of the table watermelon: the fruit are enlarged, the fruit pulp acquires a pink color, and a sweet taste appears. There is an independent segregation of bitterness and sweetness characters respectively, and forms desired by the breeders can be obtained in the second generation, i. e., forms which are sufficiently sweet but, at the same time, slightly bitter. In the second generation, there is no fruit which is entirely free of bitterness. It must be said that breeding work is made much more difficult by this bitterness of the fruit. Upon adequate selection, colocynth characters decreased quantitatively with each subsequent generation: the fruit became larger, the pink color of the pulp was intensified, and bitterness also disappeared, but the pulp still remained coarse and weakly sweet. We are of the opinion that backcrosses are absolutely indispensable in work with colocynth, and they are best carried out already in the first generation, as in work with fodder watermelon.

Crosses between table watermelon and colocynth for breeding purposes are more promising than crosses with fodder watermelon, but the work takes longer. Hybridization with colocynth is particularly promising in the creation of watermelons for storage which can be preserved for a long time without losing sugar; in fact, such forms, accumulate sugar during storage, which is a completely novel feature hitherto unknown in the assortment of table watermelons. This is illustrated by Table 5.

Table 4

INFLUENCE OF PARENT USE IN CROSS (SEED OR POLLEN PARENT) ON THE LENGTH OF THE RIPENING SEASON OF FIRST GENERATION FRUIT

Crossed species	Number of days from fruit set to maturation
C. edulis × C. colocynthoides	52
C. colocynthoides × C. edulis	68
C. edulis × C. colocynthis	60
C. colocynthis × C. edulis	94

A distinct and considerable accumulation of sugars is observed during the first two months of storage and a very insignificant loss of sugars - 0.5 to 1% - in the subsequent two to three months.

In addition to producing storage forms of the table type by hybridizing C. edulis with C. colocynthis, one also obtains many-fruited forms, some of which have sufficiently large fruit; we obtained individuals, which surpassed their parents considerably in yield (Table 6).

Table 5

CHANGES IN SUGAR CONTENT OF HYBRID FRUIT OF WATERMELON DURING STORAGE (ACCORDING TO DATA OF V.S. BONDAREVA)

Dates of analysis	First generation of backcrosses of colocynth to table watermelon varieties			
	Kubinets	Krymskii pobeditel' [Crimean Victor]	Belyi dlinnyi	Melitopol'skii 142
	sugar content of fruit (%)			
At picking time	6.52	6.73	6.64	6.15
2 weeks after picking	7.29	8.50	8.68	8.17
2 months " "	7.27	—	7.48	7.94
3 " " "	6.60	7.61	7.34	6.66
4 " " "	5.52	6.49	5.94	6.11
5 " " "	5.19	6.26	—	5.17

Table 6

NUMBER OF FRUIT AND THEIR WEIGHT IN INTERSPECIFIC HYBRIDS OF WATERMELON

Parents and F_2	Number of fruit per plant	Weight of fruit (kg)
C. edulis (Variety Vengerskii [Hungarian])	2–5	3–6
C. colocynthis	up to 30	0.1–0.4
F_1 hybrid Vengerskii × C. colocynthis	13	2–4
C. edulis (Variety Tsel'nolistnyi)*	2–3	2–4
F_2 hybrid Tsel'noslistnyi × C. colocynthis		

As was to be expected, forms of the table type, which are highly drought resistant and suitable for cultivation under desert conditions, are synthesized by hybridization of table watermelons with colocynth.

By crossing table watermelon variety Tsel'nolistnyi [Entire-leaved] with colocynth we have created a new variety, Pioner pustyn' [Pioneer of the Desert]. This variety showed an exceptional drought resistance when tested under severe desert growing conditions in the Aral desert (Chelkar), in the salty desert of Kazakhstan (Balkhazh), and under the dry farming conditions of Kirgiziya (Vasil'ev State Farm, near Frunze).

Thus, though it may be a lengthy and complicated process interspecific hybridization holds high promises for the creation of entirely new types of watermelon varieties.

* [This is the Russian transliteration for the entire-leafed variety or hybrid.]