Interspecific Hybrids Between *Beta vulgaris* L. and the Wild Species of *Beta*[1]

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Part I

Introduction

In 1925, I was sent by the U.S. Department of Agriculture to collect *Beta maritima* L. along the coasts of western and southern France, the southeastern coast of England, and the coast of Italy near the mouth of the Po River. Before traveling, I studied the collections of the genus *Beta* in the Museum of Natural History at the Jardin des Plantes in Paris, France, and at the Kew Herbarium near London, England. My attention was centered chiefly on *B. maritima*. The herbarium plants were almost universally affected by Cercospora leaf spot. A few plants found growing in Brittany, France, seemed free from the disease, as did a few plants observed near Gravesend, England. Seed balls were collected from plants, and the progenies were grown in Arlington Farm greenhouse, Arlington, Virginia. These were crossed with *B. vulgaris* L. and exposed to cultures of *Cercospora beticola* Sacc. both in the greenhouse and in the field at Rocky Ford, Colorado. The reactions of the hybrids were not impressive, and it is clear now that they were not adequately studied in the later generations. Also, some colonies of wild beets often were free from beet rust (*Uromyces betae* Tul. *ex* Kickx), whereas many adjacent stands were heavily infected. Inasmuch as this disease is often of minor importance in the U.S.A., I did not try to note it or collect samples.

In 1935, on my second visit, I studied all wild species of *Beta* in the larger herbaria, but I also studied the collections in the smaller herbaria in many of the countries visited. I went to England, France, Spain, Portugal, the Madeira Islands, the Canary Islands, Italy, Greece, and Turkey, as well as to the Netherlands and Belgium, where *B. maritima* grew on the coasts. I consulted with specialists and sugar-

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Table 1.—Sections and species of the genus *Beta*

Species	Authority	Date	Place of publication
Section Vulgares Tr.			
Beta vulgaris L.	Linnaeus	1753	Species Plantarum, p. 222
B. maritima L.	Linnaeus	1762	Species Plantarum, Second Ed.
B. macrocarpa Guss.	Gussoni	1827	Fl. Sicul., Prod. I, p. 302
B. patula Ait.	Aiton	1789	Hort. Kew, p. 315
B. atriplicifolia Rouy	Rouy	1883	Rev. Sci. Nat., Ser. 3, p. 246
Section Corollinae Tr.			
B. macrorhiza Stev.	Steven	1812	Catal. Pl. Cauc., Mem. Soc. Nat. Mosc. 3, p. 257
B. trigyna Wald. et Kit.*	Waldstein and Kitabel	1802	Desc. et Icones Pl. rar. Hung. I, p. 34
B. foliosa (*sensu* Haussk.)	*Ex siccati*	1890	*In* Sched. P. Sintenis It. Orient. No. 2750
B. lomatogona Fisch. et Mey.	Fischer and Meyer	1838	*In* Hohenacher, Bull. Soc. Nat. Mosc. 3, Enum. Pl. Talysch., p. 360
Section Nanae Ulbrich			
B. nana Bois. et Held.	Boissier and Heldreich	1846	Diag. Pl. Orient, Ser. 1, p. 82
Section Patellares Tr.			
B. patellaris Moq.	Moquin	1849	*In* DC Prod. XIII, p. 57
B. procumbens Chr. Sm.	Christian Smith	1819	*In* Horn. Hort. Hafn., Suppl., p. 31
B. webbiana Moq.	Moquin	1840	Chen. Enum., p. 16

**Beta trigyna*, as collected in Hungary and the Crimea and distributed to various herbaria, is a hexaploid. The plants collected in the Caucasus and having the $2n$ number 36 were named "*corolliflora*" by Zossimovitch. Every time the latter is mentioned in the text, *B. trigyna* is, in the writer's opinion, intended.

beet breeders in the various countries where sugarbeets are grown. I especially studied sugarbeets in Germany and Russia. I collected seeds of all recognized species of *Beta* as listed in Table 1, except for *B. macrorhiza* Stev; that was obtainable only from the Caucasus. Through the kindness of N. I. Vavilov, Institute of Plant Industry, U.S.S.R., seed balls of this species were sent to me in 1936. The plants of this species were grown in the greenhouse at Arlington, Virginia, and studied in 1937 and 1938. *Beta macrorhiza* was susceptible to *C. beticola* but did not react to curly top when viruliferous leafhoppers were fed on the leaves. Unfortunately, the plants and the seed remnant were lost when the Sugar Plant Division moved to Beltsville, Maryland, in 1942.

Beta macrorhiza did not become available again until 1958 or 1959, when F. V. Owen obtained authentic material from Sweden that had been collected in the Caucasus. The increase planted at Salt Lake City, Utah, unfortunately paralleled a row of *B. corolliflora*, and the resulting seed were either badly mixed or cross-pollinated. One packet of the 23 harvested from *B. macrorhiza* plants (Logan 8021) had only large seed balls. These seed were furnished by Dewey Stewart to N. O. Bosemark in Landskrona, Sweden, at his request for *B. macrorhiza*. I saw a plant from these seed balls in Dr. Bosemark's greenhouse. This plant conformed in every particular with my concept of the species, based on the plants grown from seed balls sent me in 1936.

Seed balls from the Bosemark plant were planted along with seed balls from Logan 8021 in the Sugar Plant greenhouse in Beltsville in 1973-74, and the plants were studied. *B. macrorhiza* is clearly a distinct species with large obtuse-ovate leaves, often slightly pruinose; the stem leaves, as well as the bracts, are large. The seed balls are very large. In my article on "The Wild Species of *Beta*" (14)[3]. I reported the confusion resulting from Transchel's (81) equating *B. foliosa* (*sensu* Haussknecht) with *B. macrorhiza* Stev. This error was followed by Aellen (1) and repeated by him in the Section on Chenopodiaceae that he furnished recently for the massive "Flora of Turkey" by P. H. Davis et al. (2). The early description given by Aellen for *B. macrorhiza* seems largely drawn from the *B. foliosa* specimen distributed to herbaria by P. Sintenis in 1890 as No. 2750. The various sites in Turkey given for *B. macrorhiza* are therefore suspect because of this confusion of species.

In my opinion, the seed-ball size characteristic of *B. macrorhiza* cannot be ignored, since *B. foliosa* (*sensu* Haussknecht) has small fruits typically segmented into threes. I had collected *B. foliosa* (*sensu* Haussknecht) at Salihli, Turkey, formerly called Salachlu (old name "Egin"). I never saw plants resembling *B. macrorhiza* in eastrn Turkey. R. K. Oldemeyer obtained *B. macrorhiza* from correspondents in Denmark and from the U.S.S.R. on his request. I. A. Sizov, Director of the Institute of Plant Industry in Leningrad, sent authentic material. The shipment was received from him in December 1957. The shipping tag indicated that the seed had been collected in the Karhas Mountains

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[3] Numbers in parentheses refer to literature cited.

(Caucasus Mountains?). This species was used by Oldemeyer (43) in his research.

In 1951 and 1971, I visited many of the places in Europe and Turkey where I had collected seeds of the wild species of *Beta*. In 1971, I tried to collect seed from as wide a range of plants as conveniently could be found.

It was too early to collect *B. trigyna* W. et K. (sometimes called *B. corolliflora* Zos.) in eastern Turkey. *B. trigyna* from Hungary and from the Crimea, as originally furnished botanical gardens and herbaria, has 54 chromosomes, whereas "*B. corolliflora* Zos." as collected in the Caucasus area has 36 chromosomes. The number of chromosomes of a plant commonly is not accepted as a valid reason on which to base a species. In the *Flora of Turkey* (Vol. II), Aellen recognizes only *B. trigyna* for plants from Hungary, the Crimea, and Turkey. Extensive collections were made of *B. trigyna* by H. Goekçora in 1952, repeating the trip he had made with me in 1951, since the seed balls as collected in 1951 did not grow. In addition, Goekçora visited Kars and Lake Van. Nearly all the seed balls collected in 1952 were viable. Thus, the pooled increase of the 1952 collection constitutes a wide range of the types growing in the area of eastern Turkey.

Table 1 lists 13 species (12, 14). Seed balls of nearly all of these will be available to specialists by July 1976. Seed balls of the various species had been furnished to plant breeders earlier so that the various laboratories could grow and use them in their research. The important difference in the present offering is the greater range covered for many of the species. Collections of many plants from as many areas as possible have been pooled and increased. I thank Gerald E. Coe for these increases. He is responsible also for the seed stocks of *B. patula* Ait. and *B. nana* Boiss. et Held. Correspondence requesting seed balls of the *Beta* species should be addressed to him: Beltsville Agricultural Research Center-West, Beltsville, Maryland 20705.

Whereas specialists dealing with the genus *Beta* may list only 7, 10, or more species, the differences among them arise (1) because *B. maritima* is or is not recognized as a species distinct from *B. vulgaris* or (2) because other species that I recognize, such as *B. macrocarpa* Guss., *B. patula* Ait., or *B. atriplicifolia* Rouy, are considered subspecies. I had earlier fully explained the inclusion of *B. foliosa* (*sensu* Haussknecht) and the error of including it as *B. macrorhiza* (14). Similarly, numbers of variants of *B. maritima* have been given species names, notably *B. adanensis* Pamuk. and *B. trojana* Pamuk. by Pamukevoğlu.

All the species of Table 1 have been grown in the greenhouse and fields at Arlington and Beltsville. All of my associates have recognized these as distinct entities—hence, the assignment of specific rank. However, the organization of the genus *Beta* is always essentially the same, the only difference being the ranking of some entities as subspecies or varieties.

Use of Variability of *Beta vulgaris* L.

An important contribution to the consideration of variability in the sugarbeet complex was given by Levan (29), who reported that in the production of polyploidy with colchicine, a number of triploids were obtained. When crossed with diploids, forms with all chromosome numbers from 18 (2×) and 27 (3×) were produced, and in the cross 3× times 3×, all possible chromosome numbers from 2× to 4× occurred. Pronounced morphological abnormalities were observed in aneuploids below 3×, whereas most plants with higher numbers of chromosomes were normal or fairly so. The study, based on a species, showed that doubling of chromosomes induces great irregularities and increases variability. In a thought-provoking study on variability, Owen (47) insisted that the occurrence in *B. vulgaris* of the forms such as sugarbeet, mangel-wurzels, table beets, and chard, as well as *B. maritima,* all of which cross readily with sugarbeet, indicates the great range of variability. Environmental variability helps emphasize genetic factors and needs to be understood and used, especially in the evaluation of degrees of resistance. Owen (46) obtained excellent examples of sugarbeets showing cross- or self-sterility. He stated that genetic variability of *Beta* should be denominated as the tool for breeding research. He stressed uniformity in size and shape of roots, color factors, sterility, compatibility relationships, and especially male sterility. Cytoplasmic male sterility is seen as most important. Owen (46) showed that when used with Mendelian characters, of which he recognized two, it could produce wholesale emasculation of plants for hybridization purposes.

Great value has come to the American sugarbeet industry from the recognition of the variability within the commercial sugarbeet (47, 13). Selection of curly top resistant varieties began in 1932 with US 1 (10). It was quickly followed by US 33, US 34, US 12, and US 22 and later by a number of productions by Carsner, Owen, Abegg, Murphy, McFarlane, and their associates in the U.S. Department of Agriculture. Plant breeders of beet sugar companies also contributed to the rehabilitation of western sugarbeet agriculture that was about to be abandoned because of the ravages of curly top.

A striking example of the value of selection from commercial stocks of sugarbeet for basic improvement in growth habit and disease resistance is shown in US 15 (15). Selections had been made in 1927 in a field of Rabbethe and Giesecke variety Pioneer that was grown at the Agronomy Farm of the New Mexico Agricultural Experiment Station under severe natural exposure to curly top. A second selection was made in 1930 under similar exposure to obtain roots for a planting for seed increase. Seed thus obtained was tested in 1932 and 1933 at Fort Collins, Colorado, for leaf spot resistance. The variety was susceptible to leaf spot and was about to be abandoned. Then C. A. Lavis and F. G. Larmer reported that in their 1932 and 1933 winter plantings in southern California, US 15 had not bolted, whereas US 1 and other curly top resistant varieties had largely gone to seed. Seed of the remnant of US 15 were increased. In 1936, abundant seed were available for fall-planted tests in the San Joaquin and Imperial Valleys of California. These proved that the variety was prevailingly nonbolting. Very shortly, it became the variety exclusively used in California for September and October plantings, to produce roots for processing by the Holly, Spreckles, and Union Sugar Companies. The degree of curly top resistance was about that of US 1 and was adequate to protect the crop until its harvest in May or June of the next year. US 15 continued to be grown until it was replaced by US 56, bred by Charles Price (49), which was more curly top resistant and also nonbolting.

US 15 was selected for curly top resistance. The nonbolting character occurred fortuitously, as did the striking resistance to downy mildew *(Peronospora schachtii* Fckl.), also called *P. farinosa,* and to beet rust (*Uromyces betae* Tul. *ex* Kickx). These diseases are important in sugarbeets grown as a crop in coastal areas in California and for seed in Washington and Oregon.

In the humid areas of the United States and in Nebraska and Colorado in the decade 1925-35, Cercospora leaf spot (*Cercospora beticola* Sacc.) was making beet growing hazardous. As a result, many factories were closed or were about to close, because many farmers would not contract to grow the crop. In Colorado, Nebraska, Minnesota, and North Dakota, the crop periodically was made unprofitable because of leaf spot. Black root (*Aphanomyces cochlioides* Drechs.) also decimated the stands in eastern areas, particularly in Michigan and Ohio. In years of abundant rainfall that should have helped the crop, loss of leaves increased from Cercospora leaf spot, and the stands tended to be poor. Loss of the original top growth and its replacement by new leaf growth caused low sucrose storage in the roots. Poor stands led to beet crops ranging from 5 to 10 tons per acre in Ohio and Michigan because of black root. These diseases made the crop unprofitable for farmer and factory.

The present sugarbeet crop represents the fruits of resistance-breeding research through which the U.S. Department of Agriculture was able to produce high-yielding, disease-resistant hybrids and varieties for use by the American farmer. These results came from selection, pure-line breeding, and the pairing of the best lines that took advantage of heterosis. Resistant and highly productive stocks of sugarbeet are now available through the continued cooperation and the breeding research of individual sugarbeet companies.

Without depreciating in any degree the work that has been done which saved the industry, it is necessary to point out that new diseases and new conditions have arisen that present important problems in beet growing. These will be pointed out and in this article the need for recourse to the wild species of *Beta* will be stressed.

Hybridization with Wild Species of the Section Vulgares

It is a very old idea that sugarbeet breeders should draw on the relatives of the sugarbeet to improve the cultivated form. Thus, Proskowitz (50, 51) very early and for some later years (52) studied *B. maritima* in the hope of improving sugarbeet production. However, the most success in using *B. maritima* was by Ottavio Munerati and his associates (39) at the Statione Sperimentale di Bieticultura at Rovigo, Italy, 1913-35. Biotypes of *B. maritima* from the estuaries of the Po River and the Adriatic Coast were repeatedly crossed and backcrossed with the sugarbeet to obtain non-bolting and leaf-spot-resistant hybrids. In 1925, I visited the Rovigo Station and saw plants from a sample plot. They were sugarbeet like and leaf-spot resistant. I was told that many hundreds of hectares of the hybrid variety were grown in Italy under severe leaf-spot conditions. Dr. Munerati declined to furnish seed of the variety or of *B. maritima* from the Po estuaries because he feared that these might introduce *P. schachtii,* which he considered a most serious disease. In 1935, I again visited Rovigo and saw in the field a large array of experiments. Leaf-spot resistance had been attained. Dr. Munerati told me that his best material had been supplied to the sugarbeet seed companies at Cesena and Mezzano, Italy, for increase and sale. Dr. Munerati gave me seed of his best variety, R 481. During 1936-45, the Munerati variety and seed stocks from Cesena and Mezzano were repeatedly tested under leaf-spot conditions at Fort Collins, Colorado. They were resistant to leaf spot, but the root yield was low. They were high in sucrose. Similar tests were conducted at New Mexico State College for curly top resistance and yield. The varieties were not resistant to curly top. At all these places and later at Arlington, the roots of the Italian varieties were cylindrical, instead of top-shaped, and tended to be fibrous or even woody. Because the varieties appeared to be deficient in tonnage, although high in sucrose, the tests with Italian stocks were discontinued.

I found a few colonies of *B. maritima* in France and England that were free from leaf spot. Plants grown from this seed were crossed with individual plants of sugarbeet, and the hybrids were tested repeatedly. Resistance was not notably improved, and the tests were given up, probably too soon. Others sought to introduce leaf-spot resistance from wild beets, as for example in the Czechoslovakian variety Dobrovice (76). The European varieties were not accepted by American growers, who preferred the varieties US 200 × 215 and US 201 × 216 that were selected from commercial varieties of sugarbeet grown under our leaf-spot conditions. Similarly, the hybrid that F. Schneider produced at Kleinwanzleben, Germany, by crossing sugarbeet with *B. maritima* was, in the F_3, beet like and only slightly rooty. It definitely showed the predominance of the anthocyanin factor, since the leaves and crown were tinged with red. Since the progeny of the variety did not show resistance to leaf spot or to curly top in our tests in 1926, 1927, and 1928, tests were discontinued. At about the same time, the firm of Gebrueder Dippe introduced Dippe Red Crown, said to be a cross of sugarbeet and mangel-wurzel. It was a productive variety but low in sugar. It was said that farmers in the United States wrote into their contracts, "No red beets."

Tjebbes (80) and Rasmussen (53, 54) conducted important studies on *B. maritima*, the former considering it a northern ecotype of *B. vulgaris* and the latter a taxonomic species. They distinguished the North Atlantic form from the smaller and annual Mediterranean type. Their work and that of Munerati et al. (39) indicated to Dahlberg (17) of the Great Western Sugar Company that *B. maritima* could be a source of genes for sugarbeet improvement and, especially from Munerati's work, for leaf-spot resistance. His translation into English of Munerati's 1922 report brought the Italian work to the attention of sugarbeet technologists. Dahlberg (16) obtained mediocre results from the F_1 of the North Atlantic wild beet with sugarbeet. Better results were obtained with the F_4's that were bulked and backcrossed with GW 3642, since the variety thus obtained was better than the Great Western commercial. Later, this work and its continuance on a large scale by Brewbaker resulted in the leaf-spot-resistant varieties used for a great many years by the Great Western Sugar Company (GW 359 and others). At a Genetics Section of the American Society of Sugar Beet Technologists held at San Diego, California, in January 1974, Brewbaker said that to obtain the GW commercial, he very early took all the available leaf-spot-resistant sugarbeet varieties and crossed these with the best Great Western commercial varieties then available. In field tests by the late G. W. Deming and by J. O. Gaskill, the Great Western varieties introduced in the early forties were not inferior to any leaf-spot-resistant variety available from U.S. Department of Agriculture breeders.

Dahlberg and Brewbaker (18) reported that the wild beet from Milpitas, California, although considered by some as an escape from *B. vulgaris,* was *B. maritima* because of so many characteristics such as its annual character, root shape, and its resistance to leaf spot. The hybrids with a resistant GW strain of sugarbeet eventually produced an F_5 hybrid with good sugar production and only about 3% tendency for bolting. It was stated that further selection was entailed, but no report of results is available.

Zossimovitch (89) reported a cross of sugarbeet with *B. maritima* in which the third generation progeny obtained after two successive backcrosses gave, as pooled seed, enough of a sugarbeet-like type that was leaf-spot resistant and higher in yield than a yield type of sugarbeet. No report was available of its use in the U.S.S.R.

After the early work of F. Schneider, Schlösser (66) reported the advance in breeding for Cercospora leaf-spot resistance as obtained by hybridization with *B. maritima*. Eventually, he had arrived at a variety almost equal to Kleinwanzleben N or E types of sugarbeet in conformation and bolting resistance, and often superior in sugar content and juice purity. He reported that yield was somewhat inferior when leaf spot was not present. He stated that the polyploid lines of the above are leaf-spot resistant. The line known as Cercopoly has given much higher root yields and sugar yield. When tested in Italy, Switzerland, Bavaria, and Turkey, the yields equaled those of the N strains of the R.

and C. Company. Schlösser stated that fangy roots and lignification were almost totally lost. Some roots exceeded the sugarbeet in sucrose percentage. Bolting did not occur.

Margara and Touvin (34) obtained hybrids of sugarbeet with *B. maritima* that showed relative tolerance to Jaunisse ("yellows"), but repeated backcrossing failed to remove such undesirable characters as low sucrose percentage or the forked-root tendency. Compared with yellows-tolerant lines from the United States, the French hybrids were superior to the imported lines, believed due to different races of the virus in France.

Bilgen et al. (4) reported transferring by backcrossing the resistance to *C. beticola* from *B. maritima* to curly top-resistant varieties by using successively US 22/4, SL 539, and McFarlane's C 663. After each backcross, the progenies were allowed to intercross. As a result, a variety with resistance to leaf spot and acceptable root weight was obtained.

In 1969, Dewey Stewart revived the idea that for progress in sugarbeet breeding, it would be necessary to go back to *B. maritima* for new genes. This was an old idea that had been abandoned, mostly because resistance to curly top and some degree of resistance to leaf spot had been obtained from existing commercial stocks of sugarbeet. By a thorough search in Europe of the colonies of *B. maritima*, Stewart found Cercospora-free plants at Wembury Bay near Plymouth, England, at Kilmore Quay, Ireland, and at Kalundborg, Denmark, whereas neighboring wild beet plants had severe leaf spot. Seed were collected at each location, and the progenies grown at Beltsville have shown fair resistance to leaf spot. Their hybrids are in the third backcross with sugarbeet, and this backcross will again be backcrossed to sugarbeet. If the backcrossing gives beet-like plants that are resistant to leaf spot and otherwise satisfactory, introduction will be made through the customary channels. G. E. Coe is cooperating in this study.

Finally, I have tried to go to *B. maritima* for genes resistant to leaf spot, assisted by Raymond Hull, Director of the Broom's Barn Experiment Station near St. Albans, England (a branch of Rothamsted Experiment Station) and A. W. D. Dyer of the British Sugar Corporation stationed at King's Lynn, England. With their cooperation and, in the United States, that of Dewey Stewart and G. E. Coe, I have arranged for two good lines of sugarbeet to flower in England to obtain massive crosses with their dense stands of *B. maritima*. The tests have been set up at Heacham, 7 miles north of King's Lynn (Snettisham Beach), and on Shotley Peninsula, Holbrook Bay (Sutton Ness), in cooperation with A. W. D. Dyer and D. Hetherington, respectively. Seed were planted in 1972. Whereas seed balls were taken from wild beets in that year, seed balls from the wild plants in the plots as set up will be mainly collected in 1975. The collections should represent the fourth generation of any hybrid. A large planting will be made of the seed balls obtained from *B. maritima* parent plants. All frankly wild types will be discarded, and only sugarbeet-like types with *B. maritima* heritage will be left. Any plants saved will be subjected to heavy exposure of Cercospora leaf spot, and only highly resistant plants will be saved. These will be allowed to interpollinate, and only beet-like plants will be saved. If, at first, seed balls are taken only from the wild parent and only recombinations are selected in the fourth and fifth generations, leaf spot resistance will possibly have been transferred, and a recombination of value will have been secured.

Hybridization with Wild Species of the Section Corollinae

The morphology and taxonomy of certain members of this section were basically researched by Scheibe (65), who studied *B. lomatogona* Fisch et Mey., *B. trigyna* W. et K., and *B. intermedia* Bunge. He concluded that probably *B. intermedia* was a hybrid of the other two species. Its authenticity had long been questioned by other systematists. *B. lomatogona* has been studied by Walther (85, 86), who collected at Eskisehir, Turkey. He recognized diploid, tetraploid, and pentaploid forms. My collections in Eskisehir did not give any pentaploids, since I could not positively determine the leaf characters as given by Walther. However, I found monocarp and polycarp types, each clump or small area being exclusively one or the other type. Scheibe (65) reported sucrose as high as 30%, not only in the parent species but in the hybrids, remarking that these exceed those of the cultivated *B. vulgaris*. He noted the frost and drought resistance of *B. lomatogona*, as well as the tolerance of salty soils. Defects are its deep roots and branching habit. The germination problems and perennial nature of the plant are considered formidable obstacles in hybridization. Scheibe speculated that since *B. trigyna* had a $2n$ number of 54, thus harking back to the Hungarian and Crimean collections, hybridization with the Section Vulgares with $2n = 18$ would not succeed. He remarked, however, that since *B. lomatogona* and *B. intermedia* show indications of resistance to leaf spot and to leaf miner, these species might be of interest to the beet breeder.

Seitz (70) made reciprocal crosses of *B. vulgaris* and *B. trigyna*, in which only the female organs of the hybrid were fertile. Causes of the male sterility were to be studied, but they were not reported. In later studies, Seitz (71, 72) confirmed his earlier finding of 36 chromosomes in the F_1 plant, but the backcross progeny had $2n = 27$. Because of the disparity of chromosome numbers in the parents, meiosis was irregular. At division, lagging of chromosomes occurred and tetrads were irregular. Pollen grains were abundant and plump before the flowers opened, but at anthesis, the anthers dried and did not dehisce. In the reciprocal cross *B. vulgaris* × *B. trigyna*, the hybrid was male sterile and only the female organs were fertile. The chromosome numbers in the F_1 were $2n = 36$ and in the F_2, $2n = 27$. Irregularities were found in the F_2. The *B. trigyna* had 54 chromosomes and a hexaploid was crossed with a diploid. In a report appearing at about the same time, Bleier (5) obtained similar results. He pointed out that the *B. trigyna* chromosomes do not pair with the *B. vulgaris* chromosomes. Unequal distribution at the poles of trivalents and univalents may result in pollen and ovules lacking a complete genome, hence sterility.

Schneider (68) and Stehlik (76) conducted research for their respective sugarbeet seed companies with hybrids between *B. vulgaris* and *B. trigyna*. Both reported lack of success, although Stehlik obtained one hybrid. Zossimovitch (88) suggested use of wild species of *Beta* for sugarbeet improvement. He hybridized *B. vulgaris* with material collected in the Caucasus (89, 90, 91). Savitsky (60) epitomized the cytological work done by Zaikovskaya (87) on the Zossimovitch hybrids which had been reported by him in 1941 and 1967. The Zaikovskaya studies indicated only a few associations between chromosomes of different species. The irregularities in the first and second meiotic divisions led in all hybrids to formation of dyads, pentads, and hexads that contained many chromosomes thrown into the cytoplasm. Sterility in F_1 hybrids appeared to be due to inviable combinations of chromosomes in their gametes, resulting from irregular meiosis.

The work in which members of the Corollinae group were used does not indicate any advance from the hybridization. The cross of *B. macrorhiza* with a fodder beet, White Giant, made by Zossimovitch (90), though it showed some evidence of heterosis, had sucrose percentages between 4.6 and 7.5. The hybrids were less winter hardy than either *B. macrorhiza* or *B. lomatogona*. Using authentic *B. macrorhiza*, Oldemeyer (43) did not obtain plants beyond F_1.

Margara (32) and Margara and Ometz (33) made the cross of tetraploid *B. vulgaris* and a tetraploid form of *B. lomatogona*, each $2n = 36$. The F_1 plants were morphologically similar to the wild parent in the juvenile stage, but more nearly resembled the sugarbeet parent at the end of the vegetative cycle. Meiosis was fairly regular. The hard fruit character of the wild parent was dominant, but the monogerm character was recessive. All hybrids showed a high degree of sterility. Use of this hybrid has advantages, because *B. lomatogona* has isolated fruits, is resistant to dryness and cold, and appears resistant to mosaic and to yellows. Continuation of cytological and genetic work was promised but has not been forthcoming.

In research at Kiev, U.S.S.R., Marincik (35) obtained fertile interspecific hybrids of both *B. corolliflora* and *B. trigyna* with sugarbeet. According to Plant Breeding Abstracts 41, Abstr. 3406, after selection, the tests in 1963-66 had shown that the sugar contents of the hybrids were 0.7 to 2.5% higher, but the yields of roots were 4 to 6% lower than those of the standard. The hybrids were highly resistant to *P. schachtii (farinosa)* but late in ripening.

The real capitalization upon interspecific hybridization of this type came from the work of Savitsky (60) in continuing her deceased husband's work. She reported the transference of the factor for curly top resistance from *B. corolliflora* to sugarbeet. Her summary reported this outstanding achievement, which may well serve as a model for other work in interspecific hybridization.

> "An F^1 tetraploid hybrid between *4n* sugarbeet and *4n* *B. corolliflora*, highly resistant or immune to curly top virus, was obtained by V. Savitsky. The b_1 and b_2 hybrid generations were produced by pollinating with diploid sugarbeets. The b_1 plants were triploid or triploid-aneuploid. Sufficient fertility in the *vulgaris-corolliflora* hybrids was obtained by the introduction of a complete diploid set of *B. vulgaris* chromosomes into the F_1 and b_1 generations.
>
> "These *vulgaris-corolliflora* hybrids are amphidiploids, i.e., pairing of chromosomes, as a rule, is autosyndetic between identical genomes (genomes belonging to the same species). In meiosis of *3n* b_1 hybrids, nine *B. vulgaris* bivalents and nine *B. corolliflora* univalents were formed. Occasionally, one or two trivalents were observed. Meiosis was quite regular; many univalents were transferred to the poles and included in the interkinetic nuclei.
>
> "First and second backcross hybrids were inoculated with the curly top virus and selected for resistance. Highly resistant and apparently immune b_2 hybrids were selected. They had two to seven *B. corolliflora* chromosomes in addition to the diploid set of *B. vulgaris* chromosomes. Resistance was due to genes on the *B. corolliflora* univalents."

Hybridization with Wild Species of the Section Patellares

It has long been recognized that the plants of Section Patellares have special attributes to contribute to sugarbeet improvement. Thus, the resistance to Cercospora leaf spot and to curly top has long been claimed. However, the resistance to curly top was denied by Murphy and Giddings (40) as a result of their exposure of *B. patellaris* Moq. at Jerome, Idaho, to field strains of curly top that could affect plants severely. It has long been known that members of the Section Patellares are either immune or highly resistant to the sugarbeet nematode (26), and the bulk of work has been to improve resistance. Possibilities of such improvement are being influenced by the claimed production of biotypes (73) of the nematode that may alter the value of interspecific hybridization. Golden (25) states that the members of the Section Patellares of *Beta* are susceptible to six species of the root-knot nematode, but reserves judgment on some forms of nematodes.

After determining that hybrids of *B. vulgaris* and *B. maritima* were susceptible to the sugarbeet nematode, Simon (74) obtained three fertile hybrids between *B. procumbens* Chr. Sm. and a Kleinwanzleben sugarbeet. Of 25,000 F_3 plants, 10% showed little or no infection. Polyploidy brought about by colchicine did not increase nematode resistance. These results were more promising than those of Schneider (69) when it was recognized that *B. procumbens* was not attacked by nematodes. He hoped that the cross might give resistance. Most of the F_2 plants resembled the sugarbeet parent and showed greater tendency to produce seed. About 1% of the plants showed few or no nematodes. No further results were reported.

The great breakthrough in the use of wild species of the Section Patellares came when Stewart (78) reported his success in crossing the sugarbeet with *B. procumbens* and his success in making the first generation backcross using sugarbeet pollen. Unfortunately, his second backcross gave sterile plants, and here the work stopped. This showing was followed by a great deal of work. The 1954 Proceedings of the American Society of Sugar Beet Technologists has several very important articles on use of species of the Section Patellares for sugarbeet improvement. For example, Gaskill (22) mated Swiss chard with *B. procumbens* and *B. webbiana* Moq. The first hybridizations had been made in 1945; his later attempts at these matings gave rise to 445 and 590 plants of hybrids with *B. procumbens* and *B. webbiana*, respectively. Six plants of the first cross and 19 of the second were classed as healthy. In his publication, the author noted:

> "Soon after the above article had been prepared, the roots of seedlings which had been grown for three months in soil infested with sugar beet nematode (*Heterodera schactii* Schmidt) were washed and examined microscopically. Specimens of the female nematode were found on 29 or 30 sugar beet plants examined and on all of the 7 chard plants in the test, but were not found on any of the F_1 hybrids—chard × *B. procumbens* (2 plants) and chard × *B. webbiana* (4 plants). Most of the hybrids were small, and the results cannot be considered as conclusive, but they do suggest that the high degree of nematode resistance, known to be a characteristic of the 2 wild species, was transmitted to the hybrids."

As another example, Oldemeyer (42) mated species of the Section Patellares with certain species of the Section Vulgares, notably *B. atriplicifolia*, a California wild (*B. maritima*), and an accession of *B. macrocarpa*. He reported that the failure of some matings resulted from embryo abortion, lack of fertilization, and inviability of the hybrid seedling. He reported that one plant, *B. macrocarpa* × *B. webbiana*, was extremely vigorous. Its growth habit was intermediate between the habits of the parents, but the flowers were borne in groups of three, four, or five, similar to those of *B. macrocarpa*. The flowers of this plant were not functional. Another hybrid, California wild × *B. procumbens*, died shortly after it began flowering. He stated that the *B. atriplicifolia* × *B. procumbens* plants would flower and others would probably die before flowering.

In another contribution, Oldemeyer and Brewbaker (44) pointed out the importance in sugarbeet improvement that would result from a cross of plants of the Section Patellares with the Section Vulgares. They stated that except for plants being carried to the F_2 by Stewart, the hybrids were inviable in the F_1. The hybrid plants from the cross with Detroit Dark Red, a table beet, with *B. procumbens* and *B. webbiana* were viable but sterile. Two hybrids of *B. maritima* × *B. procumbens* produced flowers (*B. maritima* was Plant Introduction 206411 from Turkey). One plant was highly sterile; the other plant produced a number of seeds. They reported that others of the same type would flower in 1956. The offspring resulting from pollination of the semi-fertile hybrid with sugarbeet is thrifty, and there is hope that desirable traits of the Section Patellares can be transferred to sugarbeet. The authors also reported that the attempts to obtain hybrids of sugarbeet with plants of the Section Corollinae were unsuccessful.

Savitsky and Gaskill (62) and Savitsky (57) attacked the problem of infertility in the cross of *B. vulgaris*, represented by Swiss chard and *B. webbiana*. Savitsky had determined that *B. procumbens* and *B. webbiana* each have 18 chromosomes as the $2n$ number, whereas *B. patellaris* is a tetraploid ($2n = 36$). Using material fixed at Fort Collins by Gaskill, Savitsky made important cytological studies to determine the cause of sterility. The problem was reduced to association of chromosomes of the respective species. As others had reported, there were irregularities, including multipolar spindles; thus deviation from normal division. Many nuclei with reduced chromosome numbers resulted, leading to nonviable pollen grains. Because of the high sterility of the gametes in these F_1 hybrids, there was little chance to obtain progeny from intercrosses. After exploring other possibilities, the authors inclined to the use of tetraploid plants for all future hybridizations.

Savitsky (59) reported on fixed material received from Oldemeyer and Brewbaker from the Turkish *B. maritima* crossed with *B. procumbens* for comparison with the hybrid *B. webbiana* studied earlier. Among the other findings, the cytological study revealed that only diploid gametes with a complete set of chromosomes of both species or gametes with the number of chromosomes approaching this number were viable. Haploid gametes with nine chromosomes were not viable, because they contained variable numbers of chromosomes from both species. Hybrids derived from two diploid species could not survive on the diploid base but shifted to a higher ploidy level. From these observations, Savitsky (58) suggested that, to overcome sterility in the interspecific hybrids between *B. vulgaris* and species of the Section Patellares, it might be desirable to obtain hybrids on a higher ploidy level.

Johnson and Wheatley (28) failed, after many backcrosses, to transfer sugarbeet nematode resistance in a cross of *B. vulgaris* × *B. webbiana*. Ohta (41) obtained only one feeble F_1 in the cross of sugarbeet with *B. webbiana*. Bornscheuer and Schlösser (6) thoroughly reviewed the literature. Then after 3 years of crossing experiments with *B. vulgaris* and species of the Section Patellares, they had the same difficulties as other investigators. The unthrifty hybrids were grafted on healthy stocks and brought to flower. The salient contribution of the authors was the use of amphidiploids produced by colchicine treatment to establish fertility. The authors credited other experimenters and cited Savitsky's work in their bibliography. Plants of the F_1 generation were hand pollinated. Two plants of the Erta breeding line of R. and G. were used as the pistillate forms, whereas these were pollinated by *B. procumbens* and *B. webbiana,* respectively, to obtain the F_1 generation. The F_1 seedlings were grafted on decapitated sugarbeet seedlings (measuring about 0.5 cm), and then cuttings were made later for vegetative production. In turn, each terminal axis was removed, and the bud in each axil was treated with colchicine after it grew. The plants were then grown in the greenhouse. Cytological study of the bracts revealed a strong evidence of chimeras. The chromosome number ranged from 18 to 144 [*sic*], as expected, because the treatment was made with fresh colchicine. The treated plants were exposed to flowering plants of diploid *B. procumbens* and *B. webbiana*, and tetraploid *B. patellaris*. Many seedlings were grown from the seed balls of the colchicine-treated F_1 hybrids. These, like the diploid hybrids, showed unthrifty root growth that would require grafting on a foster root. The authors thought that this experience indicated that colchicine-treated hybrids, if backcrossed with diploid or tetraploid wild and cultivated beets, could be used to transfer chromosomes from the wild to the cultivated sugarbeet.

Using the highly significant discovery of Savitsky (58), Savitsky and Price (64) mated abundant viable diploid, triploid, and tetraploid hybrids between *B. vulgaris* and the three species of the Section Patellares. They showed that if large enough numbers from the different lines were used, then grafting to a foster parent or using a bridge host was not essential. Better results were obtained from polyploid than from diploid matings. The authors showed that by using ample hybrids, resistance to the sugarbeet nematode as contributed by any of the species of the Section Patellares is a dominant character. The tetraploid hybrids of *B. patellaris* did not differ in grade of resistance from the resistant parent.

Bandlaw (3) reported at length on the physiology of *B. procumbens*, *B. webbiana,* and *B. patellaris*. Hybrids between sugarbeet and the first two named were obtained, but these did not produce roots after treatment with growth-promoting chemicals. F_1 seedlings grafted on sugarbeet stocks survived but were pollen sterile. When backcrossed with sugarbeet pollen, a few seeds were set, but these did not germinate. Similarly, Ohta (41) reported that a feeble hybrid was obtained by early grafting on a sugarbeet stock. The hybrid was sterile.

In these references, it has often been stressed that the meioses are irregular in both the first and the later generations of the intercross. In cytological studies, Walia (83,84) described the situation in the hybrid between *B. vulgaris* and *B. webbiana.* Paired as well as unpaired chromosomes were to be observed at pachytene. The occurrence of 18 univalents at diakinesis indicated no synapsis, and the apparent impression of bivalence was merely a juxtaposition of chromosomes. Univalents may fragment, as noted by other observers. Meiosis II may not occur, since dyads form after the first division. In short, all evidence points to incompatibility of the chromosomes.

A great amount of work has been done by Polish investigators, notably Filutowicz and Dalke (19) and Filutowicz and Kuzdowicz (20). They discussed the early work on interspecific hybrids. After the entire staff of the Polish research unit had thoroughly attacked the problem, a final report (in English) was issued in 1971. Reviewing their attacks on every facet of the problem would not be useful. They believed that the Section Vulgares hybridizes more readily with *B. corolliflora*, but that some other hybrids may have value. Anyone interested in the more complete, but rather futile, research conducted as a PL 480 project should write for "Final Report" (Institute of Plant Breeding and Acclimatization, Division of Sugar Beet and Other Crops, Bydgoszcz, Pl. Weyssenhoffa II, Poland).

Summary of Part I

Some other types of American work were of special advantage to the conditions in this country. The activities of the American sugarbeet seed industry to make available the curly top varieties and those having resistance to leaf spot have been mentioned. The nonbolting types have been of service in California. A new world of research was opened up by the monogerm varieties when these were used with that new tool in beet research—cytoplasmic male sterility.

Largely unnoticed and as yet not fully capitalized upon by beet breeders is the occurrence of the monogerm in some wild beet crosses. However, new sources of male sterility should be accumulated.

So far, successes have come chiefly from the interspecific crosses within the Section Vulgares. Regretfully, similar results cannot be cited for the other Sections, except that Savitsky (60) has reported transfers of curly top resistance from *B. corolliflora (B. trigyna)* to sugarbeet. Interspecific hybrids have been made to tap the resources of Section Patellares. The results until recently have not been of value. The hybrid can be made, and by use of the grafting technique or by bridging hosts, F_1 and F_2 generations can be made. With backcrossing to sugarbeet, in most plants the chromosomes do not pair. A promising development was reported by Savitsky at the 18th Meeting of the American Society of Sugar Beet Technologists in January 1974. She had obtained a *B. vulgaris-B. procumbens* trisomic and the transmission of sugarbeet nematode resistance to the sugarbeet. At the same meeting, Savitsky and McFarlane (63) reported the transmission of curly top resistance in *B. vulgaris* × Corollinae hybrids, thereby confirming the work by Savitsky in 1969. These reports indicate that new fields of improvement research may be opening up.

Part II:
Methodology and Applicable Techniques
Speeding of Generation Cycles
Wild Species of *Beta* in Relation to Haploids, Homozygous Diploids, and Tetraploids of Sugarbeet
Bridging Hosts
Grafting of Hybrids between *B. vulgaris* and Wild Species of *Beta*
Physiological Races of Pathogens
Use of Biotypes of *Beta*

Part II

Speeding of Generation Cycles

Munerati (36, 38) reported his technique for obtaining three generations of *B. vulgaris* in one year. Growing the source plants under continuous light in the greenhouse, he harvested ripe seeds in 70 days. When planted, the seed fruited in 2 months under the same light conditions. The plants had suffered from the hot summer heat, but when the seed were sown again, new seed were collected from the plants in November. The seed balls of this variety were furnished to F. V. Owen, who used the variety in his tests to speed the cycles. He found that the plants had the "B" genetic factor, a single dominant. He found the factor easy to transfer and, after a series of backcrossing, could be replaced by crossing to a plant of the desired character carrying the recessive allelomorph "b." McFarlane (personal communication) has verified that he has readily replaced the factor in California tests, when plants are grown under proper conditions. This replacement resulted in transforming the small-rooted, repeatedly backcrossed wild type to the commercial or normal sugarbeet type.

Gaskill (21) used the appropriate photoperiodic treatments to induce early transition from the vegetative stage to the reproductive phase. For 12 months he properly alternated cold exposure of partially grown seedlings with a warm period under lights. He obtained two generations of the hybrid. Although plants thus treated had 100% flowering, seed yields were not large. Lichter and Vieweg (31) also reported on using the principles discovered by Munerati (36) and Owen (48). Whereas Munerati had at first produced three generations in one year, later, by intensive additional lights and greenhouse culture, he obtained five generations in a year (37). Daylength was kept similar to that of the biennial form by Lichter and Vieweg (31). They found the method useful with hybridization of a biennial multigerm with monogerm beets. If the annual form is not homozygous for its tendency to produce seed, the number of generations may be increased. Usually, but by use of the factor for annualism, it is possible to obtain in 5 years a biennial, but monocarp, sugarbeet variety.

Gaskill (23, 24) found that fluorescent lights could be used in growth of beet seedlings while temperatures promoted rapid growth; but when seedlings were being subjected to cold conditions, incandescent lights were needed to induce the fruiting stage. The need for incandescent lights had been previously determined when fully grown beet roots were subjected to cold to induce seed stalk formation.

To shorten the time of the breeding cycle of a North European monogerm population, Takeda et al. (79) grew mother plants in the wintertime in southwest Japan and the next summer used them in crosses at Hokkaido. Sometimes they crossed or backcrossed plants twice during a cycle to reduce the production period. In the second cross in the cycle, a multigerm form of the plant was used as one of the parents, whereas in the first cross, a monogerm plant was used. As a result, the proportion of multigerm plants to monogerm plants was 15 to 1. An annual monogerm with the "B" factor was used as the nonrecurring parent in crosses with the European varieties used as recurring parents.

Wild Species of *Beta* in Relation to Haploids, Homozygous Diploids, and Tetraploids of Sugarbeet

Bosemark (8) found that of 13 haploid plants, five were produced by pollination of sugarbeet with pollen from wild species of *Beta* or from sugarbeet-irradiated pollen. Seven were found among inbred lines, and one occurred among the C_4 generation after colchicine treatment. The frequency of haploids was higher in the offspring from diploids pollinated with triploid or tetraploid pollen than in those in which diploid was pollinated by diploid. Of diploids, triploids, and tetraploids synthesized from the same haploid plant, the diploids ($2n$) and triploids ($3n$) did not differ in root weight, whereas the tetraploid roots weighted 7% less than the diploid roots. Leaf weight, however, increased with the increased number of genomes.

Haploids obviously can be used to obtain homozygous diploids. The literature has many reports of these resulting from sugarbeets crossed with wild species. Other than as a research tool, homozygous lines made possible by use of haploids do not seem to be of special value in sugarbeet breeding.

Bridging Hosts

Stehlik (77) suggested the use of wild beets for hybridizations with sugar and forage beets. The hybrids were repeatedly backcrossed to the respective cultivated forms. No report is given of any introductions. Varga (82) reported that hybrids of *B. trigyna* × *B. maritima* can be crossed with both *B. trigyna* and *B. vulgaris*. By use of *B. maritima* as a bridging species, segregations combining characters of *B. trigyna* and *B. vulgaris* have been obtained. (Evidently *B. trigyna* was the hexaploid.)

Oldemeyer (42) reported that failure of matings with several species of Section Vulgares and Section Patellares resulted from embryo abortion, lack of fertilization, and inviability of the hybrid seedlings. The matings were viable of *B. procumbens* and *B. webbiana* with *B. atriplicifolia* and with California wild and also with one accession of *B.*

macrocarpa. One hybrid, *B. macrocarpa* × *B. webbiana*, was extremely vigorous. Its growth habit was intermediate between that of the parents; its flowers were borne in groups of three, four, and five similar to *B. macrocarpa.* The flowers of the plant were not functional. Another hybrid between California wild and *B. procumbens* died shortly after flowering. One hybrid of *B. atriplicifolia* × *B. procumbens* was reported as likely to flower. No later report was given, but this work opened up the whole possibility of using bridging hosts. Gaskill (22) made a very important contribution by showing that it was possible to get viable hybrids from matings of Swiss chard × *B. procumbens* and Swiss chard × *B. webbiana.* A limited test of the hybrids showed the transfer of the character for sugarbeet nematode resistance. As reported, Gaskill fixed the material for Savitsky to study the meiotic divisions. These were irregular, and the second division did not take place.

For the most part, bridging hosts are used as a step in intercrossing of species. Thus, Zossimovitch (90) used forage beet, Oldemeyer and Brewbaker (44) red garden beet, and Gaskill Swiss chard. Others have found that *B. maritima* in its many forms may be useful.

Grafting of Hybrids between *B. vulgaris* and Wild Species of *Beta*

Use of healthy beet roots as the foster mother is helpful when the hybrid is made from a wide cross between species of *Beta,* but the hybrid itself does not produce secondary roots. This technique to obtain a viable plant was first developed by Coe (11) and was tested and used by Johnson (27) to obtain thrifty hybrids of sugarbeet and members of the Section Patellares by grafting the hybrid on a bolting type of sugarbeet. Johnson's male-sterile sugarbeets were pollinated by species of the Patellares group, and the hybrids were wedge grafted on sugarbeets about to go to seed. Each scion was cut back and held in place by twine. The seed stalk and all but one leaf of the stock (sugarbeet) were cut back. The scions grew and about 60% flowered. The sugarbeet used as stock was an annual type, but equal success came when ordinary biennial sugarbeets were used. Graftings to roots of the Section Patellares as stocks did not succeed. Pollen sterility in the successful grafts was common, but about 40% of the grafts showed normal fruiting when backcrossed with sugarbeet. The progeny from the backcross more closely resembled that of the wild parent than the sugarbeet and readily separated into monocarp fruits. Only eight seedlings grew from about 500 seed balls. These, in turn, had to be grafted for survival. Plants from the backcross generation looked more like sugarbeets, and there had been some enlargement of the primary roots.

The grafting technique for wide crosses was used considerably in Germany (30). I saw an entire greenhouse filled with *B. patellaris* scions growing on foster sugarbeet stocks. Little has been reported of fruitful results from this very promising beginning.

In contrast, grafting may not always be necessary. Savitsky (58) did not rely on the grafting technique but used many plants of the Section

Patellares, presumably crossed with a considerable array of wild beets. Her early work was confined to the many F_1 plants that were viable, and all viable plants have been on the triploid level.

Physiological Races of Pathogens

Very early, the resistance of certain members of the section Patellares to the sugarbeet nematode was recognized and attempts were made to capitalize upon it. Thus, Schneider (69) tried to hybridize *B. vulgaris* and *B. procumbens.* He obtained F_2 plants. Most of the hybrids resembled the sugarbeet but tended to produce seed the first year. He reported that 1% of the plants had few or no nematodes. No further results came from this early work. Simon (74) also found that races of *B. maritima* and their hybrids with *B. vulgaris* were susceptible to the sugarbeet nematode. Fertile hybrids were obtained from *B. procumbens* and Kleinwanzleben sugarbeet. Of 25,000 plants in F_3, 10% showed little or no infection. Artificially induced polyploidy in the Hilleshög variety and in other *Beta* species was reported under test. Shepherd (73) and Golden (25) have reported that the sugarbeet nematode is breaking up into individual families. Some of these developing on the wild species, previously considered resistant or immune, would now pose a threat to present attempts to introduce into *B. vulgaris* the genes for resistance from the Section Patellares. Such families, if increased on the hybrids, would seriously influence the problem.

Schlösser and Koch (67) reported that cultures of *C. beticola* obtained from six countries showed differences in rates of growth, in spore production, and virulence when grown on either a susceptible or resistant variety. Osinska (45) tested isolates of the fungus using spores from different areas in Poland, culturing them on 11 wild species of *Beta* and 2 sugarbeet types. Little difference was detected among the *Beta* species from artificial infection, except that no conidia formed on plants of the Section Patellares. Her work contradicted the general expectations, except that she reported the ZZ type of sugarbeet as more susceptible than the Bulgarian cultivar DK.

Solel and Wahl (75) have studied isolates of *C. beticola* Sacc. and found that they vary in appearance and aggressiveness as pathogens. In spite of uniformity of inoculation methods, although lesions did not differ in type or intensity of sporulation, the relative number of lesions differed. By distinctions in the disease reaction of various sugarbeet cultures, eight types of resistance were recognized. Single spore isolates from single hyphal tips were used in the tests. This work allowed the separation of these pathogens into three races.

US 201, resistant in U.S.A., was not resistant in Israel; in Great Britain, US 401 was less resistant than reported for U.S.A., and in Israel it was highly susceptible. Solel and Wahl (75) referred to similar conclusions drawn by Saito (56).

Use of Biotypes of *Beta*

What has been revealed so far in this review is no more than that to be expected from any consideration of a resistant variety bred against a pathogen. By their nature, all species of cultivated and wild plants react to the various types of pathogens—plant, animal, or virus—and to the environment, according to their biotypes—called by some scientists "races," "growth forms," or "varieties" (9).

Thus, the problems of the sugarbeet breeder do not differ from those of any other specialist seeking to fit a plant into its environment. Within the limits of host potentialities—its biotypes—the breeder must expose the plants widely to pathogen biotypes, seeking to obtain immunity or resistance in high or low degree, or tolerance, as in the terminology of European scientists.

The task, though difficult, is not discouraging. The advances already made are impressive in using the variability of *B. vulgaris* and in breeding to obtain curly top resistance, leaf spot resistance, nonbolting, sugarbeet nematode resistance, and tolerance of beet yellows (55, 34) and mosaic. The results of seeking new genes from the wild species, though limited as yet, are encouraging. It is a subject barely explored as of now.

Alas, the typical experience is to take one plant or one group representing a sugarbeet variety and to make one exposure to a single culture of a pathogen. If it does not happen to be the right choice, and usually such is the case, the negative result is taken as final.

The result of so many studies reported is that only 1, 2, or even as many as 15 plants tested gave hybrids, and sometimes these were promising. Usually the work stopped, whereas really a beginning was made in obtaining a desirable characteristic.

Often the disparity in chromosome numbers has interferred with or blocked the matings. The possibilities from polyploidy (60) and from use of colchicine (6) to increase chromosome numbers offer great promise. Bosemark (7) thoughtfully, yet highly critically, discussed the possibilities of interspecific hybridizaiton on *Beta* and advocated polyploidy with a definite role. He stressed the ease of obtaining matings within the Section Vulgares and the difficulty, if not impossibility, of obtaining genes for sugarbeet improvement from the species of sections more distantly related. However, the experimental work that he quoted and the occasional successes would seem to stress the possibilities and advantages that may come from the recognition of biotypes within the sugarbeet and the wild species of *Beta*.

My purpose has been to call attention to the weaknesses of former attempts at interspecific hybridization and to stress the significance of the biotypes of both host and pathogen. In my 1971 collecting trip to Europe and Turkey, I sought to collect from as wide a range of wild species as I conveniently could. Obviously, I could not hope to gather all biotypes, but at least I collected many plants from many locations within my time limits. Increases from this material have been pooled by species and are now offered freely to all sugarbeet breeders in a position to carry on research. I hope that they may augment their own arrays of the wild species of *Beta*. Each scientist is expected to have in his area the important plant pathogens to which he can expose the available wild species, as well as a wide range of biotypes from sugarbeet varieties. The plant breeder's job is to find the wild species that may offer some promise of beneficial genes. Of course, some clue must be given by this work to bring about worthwhile and persistent use of the widest possible ranges of biotypes of both host and pathogen. The value of bridging hosts and devices to speed generations must not be overlooked.

With this thought in mind, and well aware of the writer's own ineffective use of his own collections of wild species in 1925, 1935, and 1951, I extend this invitation to sugarbeet breeders. I hope that they will go forward in their research with full consciousness and recognition of the existence of biotypes. The task that is set up, though a very worthy one, is not easy; and the time required may even be a decade, not merely a year or two.

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