Plant Introductions in the Improvement of Vegetable Cultivars

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One cannot review the history of vegetable breeding without being impressed by the extent to which some of our crops are dependent on a relatively few characteristics originally derived from introduced material. Several important vegetable crops would not exist as they do today without the introduction of disease resistance and horticultural characteristics from distant parts of the world.

The early work by Orton (31) on wilt resistance in watermelon deserves mention because of its historical significance as one of the first successful efforts to breed resistance to a particular disease by crossing a commercial cultivar with an accession of widely divergent origin and type. The source of resistance was the nonedible African citron, and the 1st edible resistant cultivar was Conqueror, introduced in 1911. Subsequent work in Iowa, Florida, and California resulted in wilt-resistant introductions that have been and are now widely used in watermelon breeding projects.

The classic work on cabbage, started at the University of Wisconsin in 1910 by L. R. Jones (25) and continued by J. C. Walker (49), was with domestic cultivars. More recent work there by Paul Williams (personal communication) has resulted in the release of 5 cabbage breeding lines having black-rot resistance derived from a Japanese cultivar. He is introducing into various Brassica species the white rust resistance found in wild species. This work may provide a model for transferring other characteristics of these species to commercial types.

Sources of resistance to downy mildew in Brassica sp. have been found at Geneva in accessions from Sweden (PI 296131, 205993, 205994), Portugal (PI 189028), and France (PI 245015) and resistance to cauliflower mosaic from Denmark (PI 225858, 225860) and Iran (PI 229747). Additional sources of resistance to clubroot and turnip mosaic and tolerance to heat are listed by Dolan and Braverman (13).

Onions

A classic example of the impact that a single plant selection of foreign origin can have on an industry is the hybrid onion story. In 1925, Henry A. Jones discovered in his breeding plots at Davis, California, a unique plant in a progeny grown from 'Italian Red'. This plant, No. 13-53, was to become the most important single plant selection in the history of onion improvement. 'Italian Red 13-53' was male-sterile and for this reason was destined for extinction, had it not been for a large number of small bulblets formed in the seed head. By means of vegetative propagation and subsequent crossing and progeny testing, it was demonstrated by Jones and Clarke (24) that the male sterility in 13-53 was cytoplasmic-genetic in nature (Smmsm). It could be maintained by appropriate backcrosses to a maintainer with normal cytoplasm, but carrying the recessive gene for male sterility (Nsmns).

All of the hybrid onions produced in this country derive their cytoplasm from this single plant selection. Unfortunately, the original clone has been lost as a result of its susceptibility to yellow dwarf virus. In addition to its unique male sterility, this selection was practically immune to downy mildew. Fortunately, resistance to this disease in the scape, but not in the foliage, was transferred to 'Calred' (H. A. Jones, personal communication).

Aside from 'Italian Red', few foreign introductions have been used in the improvement of onions, perhaps because disease resistance and most of the needed horticultural characteristics are available in domestic cultivars. Resistance to thrips was reported by Jones and others (23) in 1934 in a cultivar imported from Persia and called White Persian. This source of thrips resistance is still being used in the USDA onion breeding program. During the past 3 years, more than 200 introductions have been screened by Henry Munger for resistance to onion maggots. At this time, a single introduction from Turkey (PI 344251) shows some promise (H. M. Munger, personal communication).

Muskelmelons

Powdery mildew appeared on muskmelons in the Imperial Valley of California in 1925 and caused increasingly serious losses for several years. Beginning in 1926, Rosa and Jagger (22) surveyed melon accessions from all parts of the world, and in 1928 they discovered resistant plants in cultivars from India near the muskmelon's origin where great genetic diversity should be expected. Of course, Indian cooking melons were not of satisfactory quality for dessert fruits, and they were poorly adapted to California. A simply inherited dominant resistance made a backcrossing program practical. By 1932, 'PMR 50' was ready for commercial trial (51). This first powdery mildew resistant melon was produced by crossing a resistant plant from an Indian accession with 'Hale's Best' and selecting resistant F2 plants for a single backcross to 'Hale's Best,' followed by self pollination and selection for 2 generations. Four additional generations of inbreeding and selection produced the famous 'PMR 45,' a more uniform and better quality melon that could be shipped across the country after harvest at full slip. It replaced 'PMR 50' and subsequently became a source of resistance for a long list of cultivars. 'PMR 45' was resistant only to race 1 of powdery mildew, and a second race of the fungus soon became predominant. Fortunately, resistance to race 2, found among other Indiana accessions, was combined with resistance to race 1 in 'PMR 5' and 'PMR 6,' released in 1942, and 'Campo' and 'Jacumba,' released in 1964. These sources of resistance to powdery mildew and sources of downy mildew resistance (PI 12411 and 124112) were used in the development of 'Georgia 47', 'Home Garden', 'Gulfstream', and 'Planter's Jumbo.' Lines related to 'PMR 6' were used in Texas in the development of 'Perlita' and 'Dulce'. All of the important commercial muskmelon cultivars grown today have one or more foreign introductions in their pedigrees. Disease resistance introduced from foreign sources has made it possible for this industry to exist without severe.
losses from diseases and costly control programs.

The melon story is not finished with these monumental achievements. Among the important contributions from Plant Introductions currently in use are resistance to Watermelon Virum I from an Indian accession (PI 135893) incorporated in line ‘865’; released to seedsmen by R. E. Webb in 1960, and resistance to muskmelon mosaic from an Oriental pickling melon reported by Enzie (15) and used since 1943 by H. M. Munger at Cornell University and by G. W. Bohn and R. E. Webb in the USDA. The value of this may be comparable to that of resistance to cucumber mosaic virus in the cucumber. Resistance to aphids found in an Indian accession (PI 371795) by Bohn et al. (6) is being used in the USDA melon breeding program.

**Cucumber**

Production of cucumbers for both processing and fresh market depends almost entirely on cultivars with important characteristics derived from Plant Introductions. The earliest work was with resistance to cucumber mosaic virus (CMV) from ‘Chinese Long’ discovered by R. H. Porter in 1926 (35). Later, Doolittle et al. (14) reported CMV resistance in the Japanese ‘Tokyo Long Green’. The first successful use of these sources was by H. M. Munger (30).

He developed the ‘Tablegreen’ (29) and ‘Marketmore’ series of slicing cucumbers and supplied breeding lines of processing types to researchers in Ohio, who used them in developing ‘Ohio MR 17’ and related breeding lines. These Ohio lines became the source of mosaic resistance for the work of J. C. Walker at the University of Wisconsin in the development of SMR 18 and other cultivars. This development virtually saved the processing cucumber industry in Wisconsin and Michigan in the 1950’s. The Wisconsin lines were used at Michigan State University in the development of disease-resistant, gynoecious parent lines for hybrid production and subsequently in the development of multiple disease-resistant lines by W. C. Barnes at the Clemson Station. The Clemson releases are characterized by a widely used gynoecious parent, ‘GY 14’, which has resistance to both northern and southern cucumber diseases.

A classic example of the use of foreign introductions for developing disease resistance is the work of the late W. C. Barnes at Clemson. He transferred anthracnose and downy mildew resistance from an Indian introduction (PI 197087) to commercially usable cultivars of both processing and fresh market cucumbers.

In 1954, Desmond Dolan at Geneva called the attention of a group of visiting plant breeders to a Korean cucumber ‘Shogoin’ (PI 220860) with some completely or predominantly pistillate plants. A predominantly pistillate plant selected from ‘Shogoin’ was crossed to ‘Wisconsin SMR 18’ in the Michigan State University greenhouse in the winter of 1954. Subsequent selection and backcrossing led to the development of the gynoecious line, ‘MSU 713-5’, released in 1960 (33) and later used in ‘Spartan Dawn’ (34), the first F1 processing cucumber produced with a gynoecious line as the female parent. The same source of female sex expression was used in the development of ‘GY 3’, released from the Clemson Station in 1966. These two gynoecious lines, ‘MSU 713-5’ and ‘GY 3’, were used extensively in the development of commercial hybrids. Since the release of these lines, private and public breeders in the U.S. and abroad have concentrated on the production of F1 hybrids of all types of cucumbers. The development of mechanized harvest has hastened the acceptance and use of hybrids in the processing cucumber industry. Because of their high early yields and concentrated production, hybrids are used almost exclusively for mechanized harvest, which now includes 90% of the crop in Michigan and is rapidly increasing in other areas.

Other sources available and in use by cucumber breeders are resistance to powdery mildew from Japan (PI 212233), to bacterial wilt from Burma (PI 200815 and 200818), non-bitter fruit in an accession from the Netherlands (PI 265887) and parthenocarpy from European greenhouse cucumbers.

**Squash**

In the squashes, one of the valuable and extensive evaluations was made by Hall and Painter (19) from 1956 to 1961, when they screened 280 accesses for resistance to squash bug and cucumber beetle. They found useful levels of resistance to both insects in accessions of Cucurbita pepo, C. moschata, and C. maxima. Workers in Delaware have reported resistance to downy mildew and powdery mildew in C. maxima from India (PI 135893). The incorporation of resistance to CMV in C. pepo found in an accession from Turkey (PI 176959) is in progress at Cornell University. The summer squash ‘Ranger’, released by the Clemson Station in 1967 (4), derived resistance to squash mosaic and CMV from a Turkish accession (PI 172870).

**Pea**

Tolerance, but no high level of resistance, to root rot has been found in extensive screening of the Plant Introduction collections of peas, including 800 foreign accessions and 1,680 breeding lines reported by Marx et al. (28) at Geneva. Hagedorn and Gritton (17) reported 2 accessions resistant to seed-borne mosaic and released 2 resistant breeding lines in 1971 (16). An introduction from Iran (PI 140295) was used at Geneva in the development of 3 cultivars resistant to pea enation mosaic (13). The Washington AES has reported 10 accessions from more than 1,300 screened that show a high level of resistance to a new race of wilt (3).

**Lettuce**

The early history of lettuce breeding up to about 1940 reviewed by Thompson (43) includes accounts of the development of resistance to brown blight and powdery mildew. Resistance to these diseases was found in domestic cultivars. More recently, an outstanding contribution has been the development of resistance to downy mildew, a disease that caused disastrous losses in areas where conditions favor its spread. In 1958-59, it destroyed more than 80% of the lettuce crop in the Lower Rio Grande Valley of Texas. Resistance to downy mildew was derived from a collection of Lactuca serriola, originally secured from Russia in 1932 or earlier by I. C. Jagger. Several lines derived from this source by USDA and the California Agricultural Experimental Station trace to the original cross L. serriola × ‘Imperial D’ made in 1932 (50). According to Welch (personal communication) and Leeper (personal communication), the introduction originally cited by Whitaker et al. (50) for the Russian L. serriola should be an earlier accession (PI 91532). In either case the source was L. serriola from Russia, from which 17 resistant breeding lines were made available to lettuce breeders in 1958. This source and an introduction from Turkey (PI 167150) acquired in 1949, provided material for the development by Leeper, Whitaker, and Bohn of the series ‘Valverde’, ‘Valmaine’, ‘Valtemp’, and ‘Valrio’, which constitute almost the entire Rio Grande Valley lettuce acreage.

Upon the appearance of a new race of downy mildew in the Rio Grande Valley in 1965, Leeper tested 125 accessions and found 5 (PI 273606, 276000, 250425, 274373, 274369) with resistance to the new race (Leeper, personal communication). ‘Calmar’ released in 1960, ‘Calice’ in 1971, and ‘Monterey’ in 1972 by USDA and California AES also derive resistance from among the 18 derivatives of the L. sativa × L. serriola cross made available in 1958. In 1973, ‘Calmar’ or strains derived from ‘Calmar’ occupied 65,000 acres or almost 50% of the lettuce production in California. An interesting recent development reported by Welch (personal communication) is
the discovery in 1974 of a race of the downy mildew fungus that infects 'Calmar' in the Santa Maria Valley, where resistant cultivars have been grown exclusively for the past 10 years. The race with pathogen adaptability is continuing, and a new search is underway for sources of resistance. A Dutch cultivar, 'Solita', appears to be resistant to the new race.

In the development of 'Vanguard', described by Thompson and Ryder (44), 3 accessions of L. serriola and 1 of L. virosa were used to produce the amphidiploid (4n) parent used in additional crosses to commercial types. Vanguard is the 1st cultivar in which L. virosa was used. It has found a place in late plantings in the winter desert areas of California and Arizona. Several selected strains of 'Vanguard' are now in use, and new disease resistant types are ready for release this year (Ryder, personal communication).

Lettuce mosaic resistance was found by Ryder (38) in 3 wild accessions from Egypt (PI 251245, 251246, 251247) among a collection of 200 items representing 13 Lactuca species screened at Salinas from 1959 to 1966. These have been hybridized with commercial types, and the release of the 1st mosaic-resistant head lettuce of the 'Vanguard' type will be made this year (Ryder, personal communication).

Lettuce plants resistant to cabbage looper, in an accession of L. saligna from Holland (PI 261653) have been described by Whitaker et al. (52). Dickson (11) found resistance to corky root rot in several accessions, one of which was used in crosses with 'Imperial 456'.

In use by bean breeders are sources of resistance to common blight among commercial cultivars and stated that no snap or dry bean varieties grown in the U.S. are highly resistant to common blight. His review of 1965 (48) tells about the screening program for common blight resistance in Nebraska where Coyne et al. (10) found 13 accessions of Phaseolus vulgaris with slight symptoms and 2 of P. acutifolius with no symptoms. In the same 1965 review, Walker again noted resistance to race 1 of halo blight in some domestic cultivars and the discovery of one introduction from El Salvador (PI 150414) resistant to race 2 among “several hundred”

The historical account of bean breeding by Wade (45) in the 1937 USDA Yearbook of Agriculture makes no mention of the use of foreign introductions. Walker's reviews of disease resistance in vegetable crops in 1941 and 1953 (46, 47) cite the extensive use of domestic cultivars as sources of resistance to several diseases. He noted differences in resistance to halo blight among commercial cultivars and stated that no snap or dry bean varieties grown in the U.S. are highly resistant to common blight. His review of 1965 (48) tells about the screening program for common blight resistance in Nebraska where Coyne et al. (10) found 13 accessions of Phaseolus vulgaris with slight symptoms and 2 of P. acutifolius with no symptoms. In the same 1965 review, Walker again noted resistance to race 1 of halo blight in some domestic cultivars and the discovery of one introduction from El Salvador (PI 150414) resistant to race 2 among “several hundred”
(1) in breeding for resistance to leaf mold.

There is a story in the progress reports from the Regional Plant Introduction Stations (3) about the original collection of a wild tomato plant at the edge of a sugarcane field near Trujillo, Peru, in 1929. Since its introduction, more than 100 tomato cultivars, including all of commercial importance, have derived their race 1 Fusarium wilt resistance from this source (PI 79532). According to Paul Smith (personal communication), a cross, *L. esculentum* × *L. pimpinellifolium*, made by D. R. Porter in 1934, provided the source of resistance to spotted wilt for the work of Kikuta and Frazier (27) and the eventual development of 'Pearl Harbor', 'Oahu', and others. A simple dominant gene from *L. pimpinellifolium* for resistance to collar rot was reported by Reynard and Andrus (36) in 1945. Another simple dominant for Stemphylium resistance from this species was reported by Andrus et al. (5) in 1942 and by Hendrix and Frazier (20) in 1949.

In 1965, Stall and Walter (2) reported resistance to race 2 of Fusarium wilt in an accession of *L. esculentum* (PI 126915). This has been used in Florida to develop good resistance to race 2 with a high level of resistance to race 1. This source will be of increasing importance with the spread of race 2 Fusarium wilt to other producing areas.

Another South American accession (PI 303801) has provided the source of resistance to Verticillium wilt. Recently, a high level of resistance to tobacco mosaic virus found in an accession of *L. peruvianum* (PI 128650) has been transferred to breeding lines by Alexander at the Ohio AES. He used the embryo culture techniques pioneered by P. G. Smith in making his first *L. esculentum* × *L. peruvianum* cross reported in 1944 (41).

Also available are high vitamin C content from *L. peruvianum* (PI 126946) used by Yeager (54), cold germination in at least 2 introductions from Russia, resistance to late blight in an accession from Turkey (PI 204587), nematode resistance from Peru (PI 128657), and a long list of other accessions having unique horticultural characteristics or resistance to important diseases. Finally, according to Skrdla et al. (40) nearly 3,000 accessions have been described and tested for 2 major diseases by Alexander and his associates at the Ohio AES.

**Potato**

The 20-year Progress Report of the National Program for Conservation of Crop Germplasm (3) published in 1971 reports that 113 of the 120 potato cultivars released during the past 40 years have 2 or more Plant Introductions in their pedigrees. Many resulted from the early use of European cultivars by F. J. Stevenson, Usda, and the extensive use of *Solanum demissum* as a source of resistance to late blight in work started in 1928 by Donald Reddick at Cornell University. Of the certified seed grown in the U.S., 65% is of cultivars with one or more Plant Introductions in their pedigrees. Material for potato breeders is provided by the inter-regional project (IR-1) as described by Rowe (37) in 1966.

The work with induced haploids in potato by Hougas and Peloquin (21) of the University of Wisconsin and Rowe of the USDA has facilitated crossing with diploid species. One of these, *S. phureja* (PI 225682), from Colombia, used as a pollinator, has been an outstanding haploid inducer and has been used in more than 20 countries to produce thousands of haploids. These have been hybridized with most of the 24-chromosome species representing about 2/3 of the wild tuber-bearing Solanums. Among the characteristics from these diverse sources are resistance to fungi, bacteria, viruses, nematodes, and insects. They have high dry matter, frost resistance, high protein, and good quality. If this system of bringing to our cultivated potatoes such a wealth of diverse germplasm comes into general use, one of the most important consequences will be the tremendous expansion of the genetic base upon which this important world food crop relies.

**Sweet Potato**

More than 30 introductions of sweet potato, including some from Japan, Tinian Island, Puerto Rico, and the Caribbean Collection, are listed in the same report as having been identified and used to some extent as sources of resistance to black rot, Fusarium wilt, internal cork virus, soil rot, and root knot nematode. The sweet potato cultivars Gem from North Carolina in 1964, Radcliffe from Clemson in 1967, and Julian from Louisiana in 1964 derive their resistance to wilt from an accession from Tinian Island (PI 153655).

**Carrot**

Few Plant Introductions have been used to improve carrot cultivars, although recently additional sources of cytoplasmic sterility have been received from Brazil. A high level of resistance to alternaria leaf blight was observed in our plots in central Florida in 1971 in Japanese cv. Kobuku (PI 261648).

**Spinach**

In the 1971 report on Plant Introductions in the South (4), the use of introduced spinach accessions (PI 140467 and 20026) is included in the account of the development of resistance to blight (CMV 1) and downy mildew. A Belgian introduction (PI 179590) is listed as resistant to both CMV 1 and downy mildew.

**Responsibilities of vegetable breeders**

I have presented some selected historical examples of successful use of Plant Introductions in vegetable improvement, a brief account of a few recent successes, and some promising introductions in use. A few examples of recently identified material have been mentioned. Now I want to turn to the responsibilities of vegetable breeders with regard to the Plant Introduction system. Our obligations might fit the following: use, report, preserve, credit, and add.

**Use.** In addition to surveying for specific characteristics, we should grow diverse accessions and discover other characteristics that might have potential value, of which we may be totally unaware. Imagination and initiative are needed to exploit unique, unexpected traits. Besides seeking specific and unusual characteristics, we should use these diverse materials simply to broaden the genetic base and avoid the vulnerability resulting from commercial culture of a few genotypes.

**Report.** It is our responsibility to inform the Plant Introduction Stations, and through them other breeders, of the discovery of useful characteristics. Since the value of a collection is enhanced by the accumulation of information, we should permanently record and report our observations and selections. Duplication of effort by future plant breeders can be avoided, if a permanent record of our work is available.

**Preserve.** One of the primary objectives of the Plant Introduction Stations is to preserve these collections in their entirety. Is preservation also a responsibility of the breeder? I am referring to propagation by the breeder of rare individual plants having some unique trait. The decision to propagate and preserve a selection depends on the frequency of its occurrence. The safest procedure is to propagate and preserve progenies of rare individuals of potential importance and leave the decision on permanent maintenance to workers at the Plant Introduction Stations.

**Credit.** The 4th responsibility is to give credit to the individual or station who first identified or used a Plant Introduction. The immediate parents involved in a pedigree of a recently released cultivar or breeding line may be generations and many years removed from the original source. Perhaps we should always refer to the original source and cite the first published work, when it is not convenient to trace these pedigrees step by step over many gener-
Adequate exploitation of the abundant Yeager. We are beneficiaries of a rich Pritchard, Porte, Norton, Jagger, traditions established by men like Orton, Reddick, Jones, Barnes, Walker, and would relieve us of the task of maintenance numbers, and preserved by the Plant Introduction Stations. They would relieve us of the task of maintenance and would ensure availability for future use.

From this necessarily incomplete account of the use of Plant Introductions in vegetable improvement, it must be concluded that we are following traditions established by men like Orton, Pritchard, Norton, Jagger, Thompson, Whitaker, Stevenson, Reddick, Jones, Barnes, Walker, and Yeager. We are beneficiaries of a rich heritage of plant material, scientific knowledge, and plant breeding lore. Adequate exploitation of the abundant germplasm provided by the Plant Introduction system will enable us to pass on the same kind of wealth and tradition to those who follow.

Literature Cited


