Euphytica (2007) 154:383–400
DOI 10.1007/s10681-006-9209-1

Broadening the genetic base of sugar beet: introgression from wild relatives

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Received: 6 February 2006 / Accepted: 9 June 2006 / Published online: 30 August 2006

Abstract The development of sugar beet as an economically important field crop coincided with our increased understanding of modern genetic principles. It was developed in the late 1700s from white fodder beet; therefore, the genetic base of sugar beet is thought to be narrower than many open-pollinated crops. The wild sea beet is the progenitor of all domesticated beet and cross compatible with cultivated beet (domestic and cultivated are given subspecies level in the same species). The breeding system of sugar beet is complex and the crop is biennial, which lengthens the generation time to almost 1 year. A genetic-cytoplasmic male sterility (CMS) system is utilized for commercial hybrid production. Early breeding objectives were to improve the concentration and extractability of sucrose and little emphasis was placed on host–plant resistance to insect, nematode, and disease pests. As production areas expanded, these pests limited production, sometimes severely. The first systematic attempts to screen exotic and wild beet germplasm for disease resistance were initiated early in the 20th century. Many undesirable traits from wild beet were reportedly introgressed with the selected disease resistance and it was only in the late 1900s that the use of wild beet genetic resources became common place in public breeding programs. In North America, a pivotal development in utilizing the genetic resources available for sugar beet breeding was the formation in 1983 of the Sugarbeet Crop Germplasm Committee (CGC). Since the Sugarbeet CGC identified enhancing the commercial sugar beet germplasm pool as a high priority, there has been an aggressive evaluation of the National Plant Germplasm System (NPGS) *Beta* collection. This collection now has more than 2500 accessions from within the genus *Beta*. In 2002, it was estimated that close to 25,000 evaluation data points (descriptors × accessions evaluated) describing the collection were available in the Genetic Resources Information Network (GRIN) database. Over 3000 evaluations described levels of resistance of sugar beet and wild beet accessions to 10 major disease and insect pests of sugar beet. As soon as the evaluation data are collected, they are used to select the sources for the pre-breeding programs. There is a lag time in sugar beet of 8–15 years between starting a germplasm development program and releasing the first germplasm, but successes of this program are

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available in the germplasm released to the commercial breeders. Resistance genes from wild beet for rhizomania and beet cyst nematode resistance have been commercialized.

Keywords Genetic resources · *Beta vulgaris* · Germplasm enhancement

Introduction

Sugar beet, *Beta vulgaris* L., is a relatively new crop, perhaps the first to be developed at a time when modern genetic principles were becoming understood. Its development in the late 1700s followed Andreas Marggraf's demonstration that the crystalline sugar from beet (white mangold and red garden beet) was the same sweet substance, sucrose, that came from cane. White fodder beet from Silesia (the White Silesian Beet, Fischer 1989) provided the germplasm from which early sugar beet open-pollinated varieties were derived, therefore, the genetic base of sugar beet is thought to be narrower than many open-pollinated crops (Bosemark 1979, 1989). Fodder beet was bred from garden beet, which was domesticated as a leafy pot herb in pre-Christian times and, by the Middle Ages, was used as a garden leaf vegetable, root vegetable, and medicinal herb (Ford-Lloyd et al. 1975). The wild sea beet (*Beta vulgaris* subspecies *maritima* (*B. v.* ssp. *maritima*) long has been thought to be the progenitor of all domesticated beet, and recent molecular data have confirmed this (Hjerdin et al. 1994; Jung et al. 1993; Letschert et al. 1994).

Taxonomically, the genus *Beta* is divided into four sections: *Beta* (formerly *Vulgares*), *Corollinae*, *Procumbentes* (formerly *Patellares*), and *Nanae*, represented by a single species endemic to Greece. The Section *Beta* includes the cultivated beets (*Beta vulgaris* subspecies *vulgaris*), which are divided into four Culti-groups (Leaf beet group, Garden beet group, Fodder beet group, and Sugar beet group) (Lange et al. 1999). The wild maritime beet (or wild sea beet) and cultivated beet groups are cross compatible. The Section *Beta* is indigenous to the Mediterranean area, extends westward as far as the Canary Islands, east through the Middle East to India, and north along the Atlantic coast to Scandinavia. Letschert et al. (1994) have recently revised the Section *Beta*. The wild taxa within *Beta* are an important genetic resource for disease resistance breeding of cultivated beet [*Beta* taxonomy is well reviewed by Ford-Lloyd (2005)].

The breeding system of sugar beet is complex. The crop is biennial; therefore, flowering requires vernalization, at 10°C or lower for 80–120 days coincidental with or followed by long-day photoperiod (Owen et al. 1940), which lengthens the generation time to almost 1 year. In the wild type, two or more flowers fuse in clusters producing what are called ''multigerm seedballs'', producing as many as five seedlings per seed ball. Precision sowing requires single seeded cultivars. A recessively inherited, maternal trait, known as monogermity occurs, in which only single flowers (resulting in seedballs with one embryo) are produced. In hybrid cultivars, the seed-bearing parent must be monogerm and, to provide ample pollen, the pollinator parent is usually multigerm. The seedball produced is monogerm (maternal parent fruit), but the true seed is genotypically multigerm, ameliorating the undesirable pleiotropic effect on vegetative plant growth often associated with the monogerm condition.

There are two types of male sterility: (1) genetic male sterility (inherited in Mendelian fashion on the nuclear chromosomes) (Owen 1952) and (2) genetic-cytoplasmic male sterility (CMS) (controlled by an interaction of nuclear and mitochondrial genomes) (Owen 1945). The maintainer of the CMS line (having sterile cytoplasm with recessive restorer genes—*xxzz*) is called an 'O-type'. The CMS system makes hybrid cultivar production practical. Sugar beet is normally allogamous (out-crossing), governed by a complex gametophytic self-incompatibility system, which prevents self-pollination but allows almost any two plants to cross-pollinate (Owen 1942). There is a dominant, self-incompatibility suppressor gene, that conditions self-compatibility, causing almost complete self-fertility. Self-fertility may be used in combination with genetic male sterility in population improvement programs based upon selfed-progeny performance and to develop inbred lines for hybrids (Bose-

mark 1971; Doggett and Eberhart 1968; Owen 1954).

Most modern cultivars are 2- or 3-way hybrids resulting from an inbred monogerm, CMS line (female) crossed to a multigerm pollinator. Hybrids may be either diploid (2n = 18) or triploid (2n = 27). Triploids are produced from autotetraploid (2n = 36) pollinators, in which colchicine has been used to double the chromosome number of a diploid plant. Because most parental lines are not deeply inbred, especially pollinator lines, genetic variability still occurs within sugar beet hybrid cultivars, compared to a single cross corn hybrid and self-pollinated crops such as wheat, soybean, or common bean. Until recently, the genetic structure of sugar beet hybrids was similar to synthetic hybrids in forage species, but is now approaching corn in uniformity.

The first sugar beet varieties were developed and produced in Northern Europe, in a non-humid, temperate, and relatively disease-free, environment. Therefore early breeding objectives were to increase the concentration and extractability of sucrose and little effort was placed on finding and maintaining high levels of host–plant resistance to insect, nematode, and disease pests. As sugar beet production spread east (Russia and Asia), south (Mediterranean area) and west (England and North and South America), new diseases, endemic to these areas of cultivation, were encountered, and sugar beet production was limited, in some cases severely. Plant breeders were confronted with insect, nematode, and disease pests of sugar beet for which there were no known sources of host–plant resistance (Lewellen 1992). The first systematic attempts to screen exotic and wild beet germplasm for disease resistance were initiated early in the 20th century.

Historic use of wild relatives in sugar beet breeding in North America

Other than the early successes of Otavio Munerati, who used wild beet (*B. v.* ssp. *maritima*) growing in the Po estuary as a source of host–plant resistance to leaf spot (caused by *Cercospora beticola*, Sacc.) (Munerati et al. 1913), it is difficult to document the impact of *B. v.* ssp. *maritima* germplasm in commercial breeding programs. Among the undesirable traits from wild beet introgressed with the desired disease resistance were annual life cycle, red pigment in the root, fangy or sprangled roots (interferes with harvest), elongated or multiple crowns, and low sucrose concentration and sucrose extractability (reviewed in Coons 1975; Lewellen 1992; Oldemeyer 1975; Panella and Lewellen 2005).

The United States Department of Agriculture-Agricultural Research Service (USDA-ARS) (then called the Bureau of Plant Industry) sugar beet research effort began in earnest in the early 1920s in response to the devastation caused by Beet curly top virus (BCTV) (transmitted by the beet leafhopper, *Circulifer tenellus* (Baker)), which was threatening sugar beet production in the western United States (reviewed by Panella 2005b). In 1925, ARS broadened the resistance breeding program to include resistance to the devastation caused by *Cercospora* leaf spot (CLS). This effort, which focused on developing open-pollinated varieties, marked the beginning of a long time commitment of the USDA-ARS to the research and development of sugar beet production practices and germplasm. It also awakened an interest in the potential of wild relatives of sugar beet as a largely untapped reservoir of disease resistance genes. In 1925 and 1935, George H. Coons of the USDA-ARS went on plant exploration missions throughout Europe and the near East to collect potential sources of leaf spot and BCTV resistance in wild beet and other *Beta* species (Coons et al. 1931, 1955; Coons 1953, 1975). Although there was some effort to evaluate this material, it ended up in Beltsville, MD, where storage conditions were unsuitable. When the collection was sent to Salinas, CA for regeneration by ARS scientist, John McFarlane, much of the seed was not viable but that which germinated was increased and a cursory evaluation made. Subsequent investigations found this material to possess many useful traits (e.g.; Lewellen and Whitney 1993; Lewellen 1995b, 2000b, 2006; Lewellen and Schrandt 2001; Whitney 1989a, b; Yu et al. 1999). Although during these years (1920–1960) and, to some extent, until current times, there was

world-wide germplasm exchange among some breeding programs, this was informal and few public records exist (Lewellen 1992).

In the 1960s there were major innovations in sugar beet breeding and production that came together to improve production but, also, narrowed the gene pool that commercial sugar beet breeders utilized. The concepts and genetic attributes for the production of hybrid sugar beet came from Owen's research into CMS with a genetic fertility restoration system (Owen 1954) and the use of self-fertility (Owen 1942). This hybrid system coupled with the monogerm trait discovered by Savitsky (1952), allowed for the development of higher yielding monogerm varieties that did not require the extensive hand labor to ''single'' the multiple seedlings of earlier multigerm, open-pollinated varieties. Initially, only one source for the monogerm trait and a single CMS germplasm were used, which led to a further narrowing of the diversity of hybrid combinations. At the same time, economic pressure caused producers to grow sugar beet in shorter rotations and increased acreage, exacerbating already heavy disease pressure. With the success of hybrid, monogerm seed, ARS breeders began concentrating on pre-breeding or germplasm enhancement (Bosemark 1989; Janick 1989; Smith 1993), and left hybrid cultivar development to the commercial seed companies. However, persistent problems with the introgression of undesirable traits from exotic germplasm made many plant breeders wary of using wild or non-sugar beet germplasm (Frese et al. 2001; Frese 2002; Lewellen 1992; Oldemeyer 1975).

By the 1980s, the increased pressure from insect, nematode and disease, especially from rhizomania (which was becoming a tremendous threat to global production), and a desire for greater productivity, made breeders consider *B. v.* ssp. *maritima* and other exotic sources of germplasm more seriously (Lewellen 1992). In North America, a pivotal development in utilizing the genetic resources available for sugar beet breeding was the formation in 1983 of the Sugar Beet Crop Advisory Committee. The USDA-ARS's National Plant Germplasm System (NPGS) introduced the Crop Advisory Committee (now Crop Germplasm Committee—'CGC') concept to support and aid in the management of genetic resources NPGS held. These committees were established to work with the curators of the various collections and provide an avenue for input from public and private users of the collections (reviewed by Janick 1989). Devon Doney (USDA-ARS in Fargo, North Dakota (ND)) was the first chair of the Sugarbeet CGC. He initiated an aggressive program to collect and evaluate *Beta* germplasm through a series of US collaborators within the federal, university and private sectors (reviewed by Panella and Lewellen 2005).

Recent efforts in North America to improve sugar beet using wild relatives

The initial Sugar Beet Crop Germplasm Committee consisted of scientists from commercial seed companies, university researchers, and federal ARS scientists. Its charge was to develop its own work programs, become self-sustaining, and advise the NPGS and its own crop commodity's scientific group (the American Society of Sugar Beet Technologists—ASSBT). In February, 1983, at the first meeting, the discussion centered on 4 major topics:

1. Develop a set of germplasm descriptors for the *Beta* collection that would provide useful information to the research community and commercial breeders.
2. What were germplasm acquisition and collection needs?
3. What were the maintenance needs for the US collection?
4. And, how could the *Beta* collection be evaluated, and the information be used to enhance the germplasm made available by ARS breeders to the company breeders?

What Doney was able to achieve in attacking these problems was the creation of a coalition of all of the parties in North America that were involved in sugar beet production and development. The CGC was an NPGS-sponsored committee, but it is also a committee of the sugar beet scientific society (ASSBT). Then, as now, all of

the public sugar beet breeders in North America were USDA-ARS scientists. The public breeders, the major seed companies, and university and ARS pathologists, agronomists, and physiologists were brought together to address the four questions above. Doney had a clear view of how to enhance the commercial sugar beet crop, which he likened to a pyramid (Fig. 1) that would be unstable without each layer being sound. The base was the total genetic variation in the wild, which required systematic sampling (collection), and timely regeneration for maintenance. He realized that without evaluation there would be limited use of the collection, and that after evaluation there needed to be an enhancement or pre-breeding step (Stander 1993) before the commercial seed companies would use the germplasm (Doney 1998). It was with this vision that the Sugarbeet CGC, with Doney as chairperson, succeeded by L. Panella (USDA-ARS, Fort Collins, Colorado (CO)) went to work.

Eventually (in 1993), because of a more favorable climate for seed production, the active collection was moved to USDA-ARS's Western Regional Plant Introduction Station in Pullman, Washington. The Sugarbeet CGC continues working with the curator, to reach their goal of increasing seed from 100 accessions every year (Hannan et al. 2000). There is strong industry support in this effort.

Another important charge was the development of a list of descriptors for the evaluation of sugar beet germplasm in the field and for collectors of sugar beet germplasm. Descriptors were based on those used by the International Board of Plant Genetic Resources and the International Institute for Beet Research (CGN and IBPGR 1991) and on agronomic traits of importance to the commercial seed companies. These are the descriptors now utilized in the USDA-ARS Genetic Resources Information Network (GRIN) Database—available over the internet (http://www.ars-grin.gov/cgi-bin/npgs/html/crop.pl?49). The development of germplasm evaluation strategy was discussed and descriptors were prioritized for collection purposes. It was recommended that the research community be surveyed for cooperators to screen for resistance to disease and insect pests. There has been a continuing effort to screen germplasm coordinated by the Sugarbeet CGC, and largely funded by grants from the NPGS, ever since.

Broadening the genetic base for root yield utilizing sugar beet wild relatives

In 1986, Doney (1993) began a crossing program to broaden the genetic base available to commercial seed companies. He made single crosses from 10 *B. v.* ssp. *maritima* accessions. These were crossed to male sterile sugar beet inbreds,

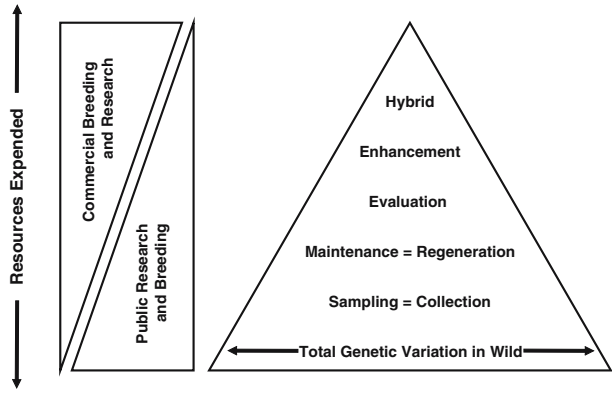

Fig. 1 The steps in a germplasm program form a Genetic Resources Pyramid with the total genetic diversity declining as the germplasm goes through selection to become a hybrid parent (after Doney 1998). The resources spent on various steps in the Genetic Resources Pyramid vary greatly between private and public researchers and plant breeders. In a productive, functioning, and dynamic program, the efforts of public and private breeders should complement one another, reduce redundancy, and cover gaps

which assured recombination by harvesting only the male sterile plants in each generation. The F_2 plants of each cross were intercrossed without selection to allow further recombination and then the populations where selected for biennial habit and conical sugar beet root type. (*B. v*. ssp. *maritima* plants generally have a fibrous root system, which is not suitable for agronomic evaluation and commercial cultivation.) Six of those populations survived four cycles of mass selection for root shape and were tested for root yield, sucrose concentration and extractability of sucrose (i.e., juice purity). Half-sib family lines were crossed to an inbred CMS line and tested for combining ability and performance. The best four families from the cross with PI 546420 (annual *B. v*. ssp. *maritima* from Greece) with L53cms were released in 1994 (Doney 1995) as unique sources of genetic variation for combining ability for root yield. It is difficult to know if much of this material has been used by commercial breeders, because, although root yield was at commercial level, percent sucrose was less than in commercial cultivars and all plants carried sterile cytoplasm.

In addition to the single crosses with *B. v*. ssp. *maritima*, Doney made crosses to a pool of representative populations of *B. v*. ssp. *macrocarpa* (now *Beta macrocarpa*), *B. v*. ssp. *patula* (now *Beta patula*), *B. v*. ssp. *atriplicifolia* (now *B. v.* ssp. *maritima*), and *B. v*. ssp. *maritima* populations from Denmark, Belgium and Ireland. Just before his retirement Doney also backcrossed his 1994 releases to a sugar beet recurrent parent. The ARS geneticist in Fargo, ND, L. G. Campbell, has continued this work and four germplasms derived from *B. v*. ssp. are ready for release, and the backcrossed populations are nearing commercial sugar beet quality and should be released within the next 3 years (L.G. Campbell, personal communication). Campbell (1992) released four high sucrose germplasms from the NPGS *Beta* collection in 1988 developed from early cultivar (Poland, Russia) or land race (Turkey) sources. Along with some of the crosses made by Doney, he currently is working with an exotic source (red globe-shaped, small canopy beet) showing resistance to the sugar beet root maggot (*Tetanops myopaeformis* (Diptera: Otitidae)).

Wild beet sources of resistance to rhizomania (caused by beet necrotic yellow vein virus)

Rhizomania (caused by Beet necrotic yellow vein virus—BNYVV) has caused major reduction in sugar beet root yield, sucrose concentration and juice quality, wherever it has occurred. It is now in every major production area of the United States. As soon as rhizomania was identified in North America, the USDA-ARS in Salinas, California (CA) began an extensive screening of genetic resources (cultivated and wild) to identify potential sources of host–plant resistance to BNYVV and to incorporate resistance into elite sugar beet germplasm (Biancardi et al. 2002). A single dominant gene for resistance, the so called ''Holly'' gene, was found by A. W. Erichsen at Tracy, CA in 1983 (Lewellen et al. 1987). This gene, named *Rz1*, conferred strong resistance to BNYVV. *Rz1* and the resistance in 'Rizor', a cultivar developed by SES in Italy (Biancardi et al. 2002; De Biaggi 1987), are the only major gene resistances identified within commercial sugar beet (Biancardi et al. 2002; Scholten and Lange 2000).

The *Rz1* allele has been easy to control and follow in breeding programs. Therefore, *Rz1* has been deployed in backcross and germplasm enhancement programs world wide (Francis et al. 1998; Pelsy and Merdinoglu 1996; Scholten et al. 1997). However, knowing that single dominant resistance genes often are not durable, additional sources of resistance were sought. With no other sources in cultivated sugar beet, other genetic resources were screened, especially, *B. v*. ssp. *maritima*, which is easily crossed with cultivated beet.

Two breeding approaches were used. The first technique was to target specific accessions and, when resistance was found, to backcross the resistance into sugar beet breeding lines. In field and greenhouse studies, using ELISA (virus titer) levels as the initial screening method (Whitney 1989b), a number of resistant accessions were identified (Lewellen 1995a, 1997). One *B. v*. ssp. *maritima* accession identified was WB42 (from Denmark), which was crossed to sugar beet parental line C37 (Lewellen et al. 1985b) and released as germplasms C48 and C79-3 (Lewellen and Whitney 1993; Lewellen 1997). The resistance

from WB42 subsequently was shown to be different from *Rz1* and conferred a higher level of resistance in growth chamber testing. It was designated as *Rz2* (Scholten et al. 1996, 1999). Although all sources of resistance conditioned by a single gene from *B. v*. ssp. *maritima* have not been determined, most have been shown to be either *Rz1* or *Rz2* (Biancardi et al. 2002). A third resistance gene, linked to *Rz1* and *Rz2* on chromosome III; recently has been reported, and designated *Rz3* (Gidner et al. 2005). *Rz3* shows incomplete penetrance, and has widely varying expression of resistance in the heterozygote. *Rz3* was mapped in WB41 (*B. v*. ssp. *maritima* from Denmark) crosses with sugar beet. It also was noted that plants, with combined *Rz1* and *Rz3* or *Rz2* in a heterozygous condition, have lower virus titer than with *Rz1* alone (Gidner et al. 2005).

Earlier, WB41 resistance was backcrossed into sugar beet and released as C79-2 (Lewellen 1995a, 1997). Further mapping evidence suggests that resistance in C79-4 and C28 (Lewellen 1991, 1995a, 1997) is different form *Rz1*, *Rz2*, or *Rz3*. C28 (PI 538250) was derived from C17 crossed to BNYVV-resistant PI 206407, which was collected in 1952 in Turkey, and classified as a sugar beet landrace, however, the only resistant plant found had definite chard (leaf beet) characteristics.

The second breeding approach was a composite approach (Doney et al. 1990), in which accessions of *B. v*. ssp. *maritima* were individually screened for resistance to rhizomania. Selected resistant plants were pooled and increased in mass, as had been done by Doney et al. (1990). No attempt was made to classify the resistance as from *Rz1*, *Rz2*, or other factors. Using this approach, long term breeding populations were synthesized. These have led to the release of C26, C27, C51, R21, C67, R23, R23B, and R20 (Lewellen 2000b, 2004c).

During the 2002/2003 season in the Imperial Valley (IV) of California, hybrids with *Rz1* resistance had rhizomania symptoms in a number of fields. This suggested that the resistance conditioned by *Rz1* had been overcome by changes in the pathogen. Laboratory, greenhouse, and field tests at Salinas in 2004 and 2005 under IV-BNYVV conditions confirmed that *Rz1* had been overcome (Liu et al. 2005; Rush et al. 2006). Tests in Minnesota also confirmed that the *Rz1* gene was not conferring high resistance to some BNYVV strains (Rush et al. 2006). *Rz2* and *Rz3* from *B. v*. ssp. *maritima* appeared to condition partial resistance to these strains, which was significantly modified by minor host-reaction genes (Rush et al. 2006). Encouragingly, enhanced progeny families of C79-9 derived from WB151 (PI 546397) (*B. v*. ssp. *maritima*) appeared to have high resistance to IV-BNYVV (Lewellen 1995a, 1997). The inheritance and allelism of this resistance has yet to be determined. Evaluations of broad-based sugar beet × *B. v*. ssp. *maritima* populations also suggested that individual plants with high resistance occurred (Lewellen 2000b). These individual plants were selected for seed production and their progeny will be evaluated for reaction to both BNYVV and IV-BNYVV.

When this new strain of BNYVV appeared in the Imperial Valley of California (Liu et al. 2005) and then Minnesota (Rush et al. 2006), there was an extensive base of germplasm populations with rhizomania resistance in place. The first germplasms screened for resistance to IV-BNYVV were these broad-based germplasm composites, which had been enhanced for rhizomania resistance and improved for sugar beet agronomic, yield, and quality traits. For continuing development of rhizomania resistant germplasm, a highly important reservoir of resistance factors is being identified in these *B. v*. ssp. *maritima* accessions and introgressed into enhanced sugar beet germplasm. However, it is obvious with the emergence of BNYVV resistance-breaking strains, that sugar beet breeders will be challenged to stay ahead of the pathogen.

Wild beet sources of resistance to leaf spot (caused by *Cercospora beticola*)

Cercospora leaf spot is a continuing problem in areas of North America when the summers are hot and humid, especially in Red River Valley of North Dakota and southern Minnesota, the Michigan and Ontario growing areas, and, less often, in the Great Plains (Colorado, Nebraska, Wyoming, and Montana). A severe epidemic may cause up to a 42% loss of gross sugar (Shane and Teng 1992; Smith and Ruppel 1973; Smith and

Martin 1978). The USDA-ARS sugar beet research program at Fort Collins began breeding for resistance in the 1920s and research has been a continuing effort at this location.

Resistance to CLS might more accurately be described as a tolerance, because tolerance or ''field resistance'' means that, although some symptoms of the disease are present, the plant still is able to perform well (Fehr 1987b, p 307). Much of the CLS-resistant germplasm in use today in North America (reviewed by Lewellen 1992), and world wide, came out of Munerati's program in Italy, in which *B. v.* ssp. *maritima* was the source of resistance genes (Munerati et al. 1913). Early varieties released by USDA-ARS were synthetics composed of a series of inbred lines from the Munerati source and inbred germplasm developed by W.W. Tracy in Fort Collins, CO. A series of CLS-resistant CMS females and O-type maintainer lines were released from the USDA-ARS breeding program at Fort Collins in 1978 (Smith and Gaskill 1979). The loss of vigor and subsequent difficulty in seed production due to the continual inbreeding has been a major concern (Coons et al. 1955; McFarlane 1971; Panella 1998; Panella and Frese 2000). The use of hybrid varieties has helped, but seed production on the highly inbred O-type males and CMS females remains a problem. Also as commercial hybrid parents become more inbred, the germplasm base from which these inbred parents are developed must have the diversity necessary to provide for maximum gain through heterosis.

In earlier CLS-resistant germplasm from Fort Collins, an estimated 4 or 5 genes are responsible for CLS resistance (Smith and Gaskill 1970), and broad-sense heritability estimates ranged from 12 to 71% (Bilgen et al. 1969), with narrow-sense heritability estimates of about 24%. An estimate of 44–62% of the variation was due environment in this test (Smith and Ruppel 1974). The large environmental variation has made it difficult to enhance resistance through mass selection in natural epiphytotics and to incorporate high levels of leaf spot resistance into varieties with superior agronomic performance (Smith and Campbell 1996).

Because CLS-resistances in sugar beet is quantitative with large environmental effects, more experimental effort is needed to discern differences among plants than would be with a qualitative resistance (Geiger and Heun 1989). In Fort Collins, the ARS breeding program uses a recurrent selection scheme to combine CLS-resistance and agronomic quality traits in a single population. Progeny testing is necessary and, although selfed progeny testing is the most efficient type (Fehr 1987a), greenhouse selfing under bags does not always produce sufficient seed on a single plant for testing. Therefore, half-sib crossing also may be used. In a normally outcrossing plant like sugar beet, the use of genetic male sterility (*aa*) (Owen 1952), combined with a gene for self-fertility (S^f)(Owen 1942) can be used to produce selfed progeny, while assuring intercrossing of selected selfed-families (Desprez and Desprez 1993; Hecker and Helmerick 1985). These populations can be used in a reciprocal, recurrent selection scheme (Doney and Theurer 1978). In addition, they can be used to build heterozygous base populations, to which additional sources of genetic variation can be added and elite lines can be continually extracted (Bosemark 1989), and to which, additional sources of genetic variation can be added. Because the self-fertility gene allows for up to 95% self-pollination, if individual, un-bagged plants are allowed to pollinate in the greenhouse, and no effort is made to blow the pollen from plant to plant, most of the seeds on male fertile plants will be selfed rather than cross-pollinated.

The screening of the USDA's NPGS Beta collection started by the Sugarbeet CGC in 1985 included resistance to leaf spot and this evaluation has continued to provide performance data on many of the accessions. Additionally the Federal Centre for Breeding Research on Cultivated Plants (BAZ)—Gene Bank (in Braunschweig, Germany) developed an International Data Base for Beta (IDBB) which contains data on the over 9000 accessions located in more than 20 gene banks around the world (Panella and Frese 2003). There were a number of these accessions that, when evaluated, showed some resistance to leaf spot during the early screening process (Panella and Frese 2000). Although currently there is a durable source of resistance to leaf spot, because of low heritability and multiple gene action, it is difficult to transfer. In addition,

broadening the genetic base of the enhanced sugar beet germplasm might lead to novel genes for resistance to CLS transgressive to the currently available tolerance to CLS. Simply defined, transgression is when a population contains individuals with phenotypes that are beyond the phenotype found in the parents of the population (deVicente and Tanksley 1993).

Genetic male sterile, self-fertile sugar beet parents were crossed to 15 non-sugar beet parents showing resistance to *Cercospora* leaf spot. Populations have been random-mated (using genetic male sterility) or bulk increased for two cycles without selection to allow recombination and then selected with low selection pressure for bolting resistance, and root type. Early generation testing before selection for leaf spot resistance showed higher levels of resistance when compared to a susceptible check germplasm. Currently the most advanced populations are in a recurrent selection program with progeny testing (selfed and half-sib) to select families with a sugar beet plant type, disease resistance, and as near commercial levels of sucrose production as possible. They will also be evaluated for resistance to other pests and diseases. Sometimes resistance to other insect, nematode, or disease may occur even if not selected for.

This first step in creating long range breeding pools (introgression of genetic diversity and leaf spot disease resistance genes from wild germplasm) is completed, and enhanced germplasm should be ready to release within the next 3 years. As the enhanced germplasm is moved into a recurrent selection pool of more advanced germplasm, it also will be backcrossed to rhizomania resistance germplasm with higher sugar to continue the improvement process and move the germplasm closer to commercial quality. Throughout this process an attempt is made to maintain a population size that will minimize extreme inbreeding, which can make seed production difficult.

Other breeding programs utilizing wild beet genetic resources

Resistance to yellow wilt

Yellow wilt is potentially one of the most destructive diseases of sugar beet. It only occurs in South America where it causes damage to the Chilean sugar beet industry. Yellow wilt is thought to be caused by a Rickettia-like organism (Hoefert 1981). The possibility of introduction of this disease organism and its leafhopper vector, *Paratanus exitiosus* Beamer, to other countries, prompted a cooperative breeding program involving scientists from the USA, Chile, and The Netherlands to develop resistant germplasm (Gaskill and Ehrenfeld 1976).

Intermediate or moderate resistance was found in wild and weedy beets growing in Chile. Because *Beta* is not endemic to the Western Hemisphere, these wild beets were thought to be escapes from cultivated beet that may have been outcrossed to *B. v.* ssp. *maritima* during seed production in Europe. Higher, but still moderate levels of resistance were identified in accessions of *B. v.* ssp. *maritima* (e.g., WB178, PI 546403, collected at Wembury Bay, UK) and resistance was introgressed into sugar beet. Pools of the most resistant yellow-wilt resistant selections from all sources were submitted to the NPGS gene bank and assigned accession numbers (e.g., selection 83W304, F_5(C17 sugar beet × *B. v.* ssp. *maritima*), NSSL No. 189776, PI 610406) (McFarlane 1984).

Nematode resistance

The sugar beet cyst nematode (SBCN) (*Heterodera schachtii* Schm.) is considered to be the most important soil-borne pest of sugar beet worldwide. Efforts to identify *Beta* genetic resources and develop resistant sugar beet have been under way for at least 90 years (Yu 2005a). Until recently, the best hope for high SBCN resistance or immunity seemed to be the transfer of resistance from the *Procumbentes* section of *Beta* (*B. procumbens*, *B. patellaris*, and *B. webbiana*) (Savitsky 1975). These species are outside the primary gene pool of sugar beet and gene transfer requires the translocation of a chromosome fragment from one of these species into the sugar beet genome. A terminal translocation from *B. procumbens* to sugar beet carried a gene, which seemed to have solved this problem (Jung et al. 1994; Kleine et al. 1995). Sugar beet carrying this $Hs1^{pro-1}$ gene is nearly immune to

SBCN (Savitsky 1975; Heijbroek et al. 1988). Commercial hybrids containing *Hs1*$^{pro-1}$ on the translocated chromosome fragment always have a significant yield penalty in the absence of severe nematode infestations. This yield drag is likely due to deleterious genes linked to *Hs1*$^{pro-1}$ on the terminal translocation on chromosome IX, or possibly gene regulation anomalies (Heller et al. 1996). This limits the immediate usefulness of this alien source of higher resistance. The literature on nematode resistance involving transfer from the *Procumbentes* section has been reviewed (Yu 2005a).

More recently, due to the problems associated with *Hs1*$^{pro-1}$, breeders have seriously reevaluated the partial resistance to SBCN known to occur in *B. v.* ssp. *maritima* (Heijbroek 1977). Commercial hybrids utilizing one *B. v.* ssp. *maritima* source of resistance have been developed and recently came to market in California ('Beta 8520N', Betaseed, Inc.), and Europe ('Pauletta', KWS, GmBH). Field and greenhouse evaluations in California have shown that the Beta 8520N resistance protects against yield loss due to SBCN and has significantly lower cysts and larvae counts than current commercial hybrids (Lewellen and Pakish 2005).

At Salinas within on-going population improvement programs in which a broad base of *B. v.* ssp. *maritima* germplasm is being introgressed into sugar beet (Lewellen and Whitney 1993; Lewellen 2000b), sources of apparent moderate resistance have been identified and selected (Lewellen and Pakish 2005). From WB242 (PI 546413) originally collected in the Loire river estuary in France, moderate resistance was known (Heijbroek 1977) and has been introgressed into breeding lines and populations including CN12 (PI 636338), CP07 (PI 632288), and CP08 (PI 6322889) (Lewellen 2004b, 2006). From a *B. v.* ssp. *maritima* accession (N499, PI 599349) obtained from a European seed company in 1994, population CN72 (PI 636339) was developed (Lewellen 2006). Greenhouse and field tests in infested soil indicate that moderate to high SBCN resistant plants segregate within these materials (Lewellen and Pakish 2005).

The *B. v.* ssp. *maritima* collection that was housed at Salinas in the 1980s was used to produce a broad based population called R22 (PI 590791) and released as C50 (PI 564243) (Lewellen and Whitney 1993) and then as C51 (Lewellen 2000b) after further improvement for sugar beet-like traits and resistance to rhizomania and virus yellows. C51 and extractions from C51 were found to segregate for resistance to SBCN in field trials in the Imperial Valley of California. One backcross derived progeny family performed well, especially under SCBN conditions, and was released as C927-4 (PI 636756) (Lewellen 2004d). From C927-4, further S_1 progeny tests were used to select for homozygousity to SBCN resistance and partially inbred line CN927-202 (PI 640420) will be released in 2006. From other broadly based sugar beet × *B. v.* ssp. *maritima* populations partially inbred, nematode resistant lines CN926-11-3-22 (PI 640421) and CN921-306 (PI 640422) also will be released in 2006.

Screening of the NPGS *Beta* collection's genetic resources has indicated a number of accessions with resistance or segregating for resistance to SBCN. The USDA-ARS breeding and genetics program at Fort Collins, CO has begun a collaborative effort with the USDA-ARS scientists at Salinas, CA to cross these into improved sugar beet germplasm. Three were biennial sugar beet landraces collected in the 1940s and 1950s, PI 142808, PI 142809, and PI 232894. There were also four annual types that showed resistance, PI 357354, PI 518303, PI 546413, and PI 504180. PI 546413 (WB242) was used in the Salinas program as a source for a number of disease resistances including nematode resistance and was used as a resistant control during the testing procedure. Between 2002 and 2005 these accessions were reevaluated for resistance and selected, resistant individuals were crossed to rhizomania resistant germplasm. Currently, F_2 and F_3 populations are under observation in the field in Salinas. Individual plant crosses were made with resistant selections and some of the populations being produced will be used in inheritance and marker studies. Allelic relationships among the SBCN resistant germplasms are being investigated in a joint research project among the USDA-ARS laboratories at Salinas (CA), Fort Collins (CO), and Fargo (ND).

In warmer temperate areas, root-knot nematode (RKN), *Meloidogyne* ssp., may cause severe

damage to sugar beet. In an extensive search within the sugar beet germplasm, no high levels of resistance were found. An evaluation of available *B. v.* ssp. *maritima* germplasm revealed two unique sources (single gene) of resistance (Yu et al. 1999). From WB258 (PI 546426), originally collected in the Po Delta of Italy, the germplasm Mi-1 was developed and then released 1997 (Yu 1997). Additional germplasms were developed from this source (M1-2, and M1-3) (Yu 2002) and Yu et al. (2001) identified an isozyme marker, PGM, linked to this resistance gene. M66 was derived from WB66 (PI 546387) and released in 1996 (Yu 1996). Further improvement of this source of resistance led to the release of germplasms M6-1 and M6-2 (Yu and Lewellen 2004). Weiland and Yu (2003) used bulked segregate analysis to identify a CAPS marker linked to the root-knot nematode resistance gene from WB66. The RKN resistance genes identified to date provide resistance to all species of *Meloidogyne* tested (Yu et al. 1999). This effort to develop RKN resistant sugar beet has been reviewed by Yu (2005b).

Resistance to powdery mildew

Powdery mildew of sugar beet, caused by *Erysiphe polygoni* DC (syn. *E. betae* Weltzien), became widespread throughout North American production areas in 1974 (Ruppel et al. 1975). Ever since, it has required chemical control, especially in the more arid growing areas of the western USA with a long growing season. Sugar beet cultivars and germplasm developed before this time in North America (e.g., the BCTV resistant material) were, for the most part, highly susceptible, having had no natural exposure and, therefore, no unintentional selection for tolerance or resistance (Whitney et al. 1983). Commercially useful resistance was found within the cultivated sugar beet germplasm base and developed (Lewellen et al. 1985a; Lewellen 1995b). This resistance was primarily moderate or slow-mildewing type, and no major genes for resistance have been found in sugar beet.

The *B. v.* ssp. *maritima* collection that was housed at Salinas, CA, was screened for resistance to *E. polygoni* (Whitney 1989a) after the epiphytotic of 1974. A continuum of reaction to *E. polygoni* was found within this wild beet accessions, including accessions that possessed near-immunity, or contained individual plants with near-immunity. Two of these *B. v.* ssp. *maritima*, WB97 and WB242, became the basis of a powdery mildew resistance breeding project. WB97 (PI 546394) was obtained in 1968 and WB242 (PI 546413) was received in 1974. From WB97 and WB242, breeding lines CP01 and CP02 were developed and released (Lewellen 2000a). Subsequently, after additional backcrosses to sugar beet, intra-line selection, and population improvement, breeding lines CP03–CP08 were released (Lewellen 2004a, b).

The powdery mildew resistance from both wild beet sources was inherited as a single dominant gene, designated *Pm* (Lewellen and Schrandt 2001). It has not been determined if the genes from WB97 and WB242 are identical. The *Pm* gene from WB242 has been linked with molecular-genetic markers and mapped to chromosome II (Janssen et al. 2003; Weiland and Lewellen 1999).

Development of smooth rooted sugar beet

Harvest, transport, and disposal of soil is unavoidable from root crops, and undesirable because of the cost of transport and disposal, and the risk of moving soil borne pathogens to uninfested fields. The so-called 'smooth root' (SR) trait is derived from hybrids between sugar beet and garden (table) beet. This can reduce soil up to 50% depending on soil type and moisture content. Early development of SR has been reviewed in the literature (Coe and Theurer 1987; Theurer 1993). Material developed by G.W. Deming at Ft. Collins, CO, was shared with G.E. Coe at Beltsville, MD, who after 12 generations of intercrossing and selecting among crosses, combined SR with resistance to Aphanomyces or CLS derived germplasm such as SP6322-0 (Coe and Hogaboam 1971). Coe released SP8030 (PI 590699) segregating for SR but with acceptable sucrose yield in 1980, followed by stable SR populations SP8531 (unregistered) and SP85700 (PI 590776) in 1985. However, sucrose content of these latter releases had not kept pace with

commercial hybrid levels, and J.C. Theurer, followed by J.W. Saunders and J.M. McGrath at East Lansing, MI continued working to develop high sucrose pollinators with acceptable sucrose yield for the eastern North American growing region. Eight relatively broad-based SR germplasms have been released since 1990 [SR80 (PI 607898), SR87 (PI 607899, SR93 (PI 598075), SR94 (PI 598076), SR95 (PI 603947), SR96 (PI 628272), SR97 (PI 628273), EL0204 (PI 632750)] (McGrath 2003; McGrath and Lewellen 2004; Saunders et al. 1999; Saunders 2000; Saunders et al. 2000a, b), each with the SR trait essentially derived from SP85700 and various improvements in the degree of SR, sucrose concentration, yield potential and disease resistance (primarily for Aphanomyces and CLS). Rhizoctonia crown and root rot resistance is low in SR lines, and germplasms EL53 and SR98 with moderate resistance to *R. solani* (AG2-2) will be released in 2006.

Resistance to Aphanomyces

Aphanomyces cochlioides (Drechs.) causes seedling damping off, which can result in poor crop establishment in the field (Coons et al. 1946). A fundamental approach to control *Aphanomyces* has been resistance breeding (Panella 2005a). Resistance to *Aphanomyces* is heritable and dominant (Bockstahler et al. 1950). The genetic background of resistance is narrow, due to selection from among an intercross population derived from eight multigerm sugar beet germplasms. Genes from *B. v.* ssp. *maritima* may supply new resources of resistance. Field evaluation of 114 accessions (from the NPGS *Beta* collection) and 6 USDA-ARS East Lansing germplasms in a natural infection demonstrated differences among accessions in emergence and stand persistence when compared with the same plot design in adjacent unaffected ground. Seventeen of these lines had survival rates as good under high disease pressure as low, although their performance, as judged by vigor, suffered in the high disease plots. An additional 4 accessions in the GRIN database are characterized as highly resistant to *Aphanomyces*.

Two biennial accessions of *B. v.* ssp. *maritima*, PI 546409 (WB185) and PI 540625 (WB879), characterized as resistant to *Aphanomyces* have been advanced in the pre-breeding program at East Lansing, MI. Single cross hybrids were made using genetic male sterile, self-fertile sugar beet parents. Individual male sterile plants were harvested and derived families were self-pollinated for two generations. The WB879-derived population was mapped with molecular markers, and selfed seed from individual plants was tested in an in vitro 3-week-old seedling *Aphanomyces* assay (Yu 2004). Results suggested two loci were involved in 'non-vigor related' resistance, with broad and narrow sense heritabilities of 0.67 and 0.61, respectively. Seed from resistant progeny were intercrossed, and populations are undergoing further backcrossing to sugar beet with selection for root shape for eventual release.

Additional pre-breeding populations using PI 546409 and WB879 have been constructed using disease nursery evaluation and inter-pollinations with SP6822. Most pre-breeding lines showed highly branched (sprangled) roots, and many lines had brown surface lesions, sometime deep, indicative of chronic *Aphanomyces* symptoms, however, segregation for *Aphanomyces* reaction was evident. Selections were based on lack of extensive visual disease, conical typical sugar beet root shape, and root yield. One family (of SP6822 × WB879) showed negligible *Aphanomyces* disease symptoms, and had a nicely shaped taproot. Stand counts taken at 20 days post emergence were significantly ($P = 0.05$) higher than most populations. Forty-one of approximately 150 roots harvested showed lesions < 1–5 mm restricted to the lenticel regions. This family may represent a source of near-immunity to *Aphanomyces*. Release of improved root shape germplasm from these materials is anticipated in 2006.

Improvement of seed germination in saline conditions

A simple in vitro germination protocol was developed consisting of germinating seeds directly in an aqueous solution and counting the number of radicles emerged (McGrath et al. 2000 and unpublished). One-hundred seventy-four accessions of *Beta vulgaris* (65 ssp. *maritima* and 109 ssp. *vulgaris* (sugar beet)) were germinated

both in a salt solution (150 mM NaCl as the stress condition) and in hydrogen peroxide (88 mM as the non-stress condition). The ratio of germination in these two conditions was taken as the measure of salt tolerant germination. Nearly 40% showed no tolerance (i.e., no germination), over half showed marginal salt tolerance, but approximately 10% demonstrated reasonable germination in salt solution. Of these, seven accessions (Ames 3051, PI 140360, PI 169023, PI 169030, PI 266100, PI 562600, PI 562601) showed similar germination (>80%) in both solutions, and plants from them have been crossed in the greenhouse with a genetic male sterile, self-fertile, salt-sensitive sugar beet.

Discussion

Currently, the USDA-ARS NPGS *Beta* collection includes everything from wild relatives to heritage open-pollinated varieties and germplasm registered in *Crop Science*. Since the Sugarbeet CGC identified broadening and enhancing the commercial sugar beet germplasm as a high priority, there has been an aggressive evaluation of the NPGS *Beta* collection. This collection now contains more than 2500 accessions from within the genus *Beta*. In 2002, it was estimated that approximately to 25,000 data points (descriptors × accessions evaluated) describing the collection were available in the GRIN database. Over 3000 evaluations characterize levels of resistance of sugar beet and wild beet accessions to 10 major disease, insect, and nematode pests of sugar beet (Panella and Frese 2003). The evaluation has focused on wild relatives in the primary gene pool, and many *B. v.* ssp. *maritima* accessions have been regenerated and evaluated.

Although this discussion has focused on research and pre-breeding in North America, there continues to be a strong international collaboration among seed companies and public researchers. In Europe, public and private plant breeders, working collaboratively through the IIRB Genetics and Breeding Working Group, are developing ''Doggett'' buffer populations (Doggett and Eberhart 1968) to introgress wild beet sources of disease resistance into the sugar beet gene pool (described in Frese et al. 2001; Frese 2002). Additionally, in Europe, evaluation funded through the European Union project—GENRES CT95 42 evaluated between 300 and 700 accessions for resistance to seedling diseases (caused by *Aphanomyces cochlioides*, *Phoma betae*), leaf diseases (caused by *Cercospora beticola*, *Erysiphe betae*, Beet yellows virus, Beet mild yellowing virus), and root diseases (caused by Beet necrotic yellow vein virus and *Rhizoctonia solani*) (Luterbacher et al. 2004, 2005; Panella and Frese 2003; Panella and Lewellen 2005). Private and public plant breeders in Europe and throughout the world are introgressing these novel sources of disease resistance into sugar beet (Asher et al. 2001; Biancardi et al. 2002; Luterbacher et al. 2000).

In addition to the collaboration in evaluating material in the gene banks, there have been close to 40 plant exploration missions, often joint ventures by different countries, to acquire new accessions. Working with the host countries over the last 20 years, the USA has sponsored collections in Armenia, Belgium, Dagestan, Egypt, France, Greece, Ireland, Italy, and Sardinia. As germplasm has been collected, the evaluation process has continued and fed into enhancement programs.

What has made this effort so successful with the sugar beet crop? There has been a coalition of all of the interested parties, and communication among them has been facilitated through the Sugarbeet CGC. The evaluators, many of them ARS scientists but also industry and university researchers, have worked closely with the ARS scientists involved in the germplasm enhancement. In this way, as soon as the evaluation data are collected, they are utilized in the pre-breeding programs. There is a lag time in sugar beet of 8–15 years between starting a germplasm development program and releasing the developed germplasm, and we are just beginning to see the benefits of this program in the germplasm being made available to the commercial breeders.

Where the sugarbeet CGC should be headed in the next 15 years?

In 1996 the Sugarbeet CGC revised the ''Report on the Status of *Beta* Germplasm in the United States'' (Panella 1986). The ultimate goal of the

germplasm effort is to enhance and develop superior germplasm for the producer (grower) that will insure a continued, viable industry. Four priorities were listed: (1) seed regeneration, (2) germplasm collection, (3) germplasm evaluation, and (4) germplasm enhancement. Seed regeneration is the most vulnerable link in the sugar beet germplasm program. Without it, collection and evaluation would be of little value. Native populations of wild beet and their relatives are in danger of extinction and, therefore, need to be collected from politically sensitive areas when the opportunity arises. Evaluation is the first necessary step in utilizing a well-maintained collection. Germplasm enhancement is the step that develops germplasm that company breeders can utilize. And the germplasm *must be utilized* to develop superior germplasm for the producer (grower) and to insure a continued, viable industry into the future.

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