17 Potential of Genetic Resources and Breeding Strategies for Base-broadening in *Beta*

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Introduction

In Europe, cultivated forms of *Beta* (leaf beet, garden beet, fodder and sugarbeet) are grown on more than 5.6 million ha, to which can be added approximately 550,000 ha in North America; 600,000–670,000 ha in China (with a promising production and market potential for sugarbeet); and a number of smaller areas in Chile, Egypt, Iran, India, Japan, Morocco, Tunisia, Turkey and Syria. Altogether, sugarbeets are grown on about 7.5 million ha worldwide. Breeding efforts are focused on the sugarbeet crop, while leaf, garden and fodder beet breeding is of regional importance only.

The genus *Beta* is native to Europe and adjacent areas. Sections *Nanae* (Greece) and *Procumbentes* (Canary Islands) have a limited distribution area, while wild species of section *Beta* occur along the coastline from the south of Sweden to Morocco and from the Canary Islands to Iran. Section *Corollinae* occurs at altitudes higher than 800 m. It has a large distribution area in Turkey and neighbouring countries. The centre of diversity is probably located where the species distribution of sections *Beta* and *Corollinae* overlap (eastern Turkey and the western part of Transcaucasia). The domestication of beets probably started in the Euphrates and Tigris region and continued in Turkey and Greece, from where cultivated beets were introduced to northern Europe (Boughey, 1981). Cultivated beets have occurred in China since the 5th century (Sun Yi Chu, 1994) and also in Arabic countries.

One of the youngest cultivated forms, the sugarbeet, has become a cash crop of worldwide importance which has been cultivated on a large scale only since 1811, when Napoleon decreed that beet should be grown for sugar. As the sugarbeet was probably selected from one single cultivated population only, the 'White Silesian', the genetic base of the crop is supposed to be very narrow. The 'White Silesian' beet had a rather low sugar content. However, the German scientist Achard considered the good root shape of this fodder-beet-like type as a favourable trait and started to select within this population for higher sugar content and yield. The sugar content increased from 4% to 16.5% between 1784 and 1981 (Winner, 1981).

Before 1960, open-pollinated multigerm varieties were developed using family selection methods and the breeding material had a comparatively broad genetic variation (Desprez and Desprez, 1993). Compared to potato, barley and other economically important crops, sugarbeet did not seriously suffer from pest and disease attacks or adverse environmental conditions in the main production areas (Lewellen, 1992). Though almost all beet pests and diseases were already known, the sugarbeet crop was considered as a relatively healthy crop until the 1960s. However, because of the growing acreage, the sugarbeet was increasingly cultivated in short crop rotation, amplifying disease problems. During the 1960s the rising cost of hand labour became an even more pressing problem. The ordinary sugarbeet seed ball contains three to four seeds; seedlings emerge in clumps and had to be thinned by hand. Savitsky (1950) found in a seed field of about 1.5 ha one monogerm, homozygous plant. This character was essentially inherited by a single recessive gene, which became of great economic importance in sugarbeet breeding and production. Lines derived from that plant, such as SLC101 (Savitsky, 1952), were extensively used in breeding programmes. In 1942 Owen (1954) discovered cytoplasmic male-sterile germplasm. After the Second World War, sugarbeet breeders focused their work on the development of monogerm, cytoplasmic male-sterile hybrid varieties with a high sugar quality, a high yield of recoverable sugar (Oltmann *et al.*, 1984) and a good level of field resistance to diseases. Only one monogerm line (C562) was resistant to bolting and all of the first monogerm varieties from the Hilleshög company, which reached more than 60% of the European market (cv. 'Monohill' and others), were derived from this line. In addition, all hybrid varieties were based on a single source of cytoplasmic male sterility, the Owen cms (Owen, 1948; Bosemark, 1979). After the introduction of cytoplasmic male sterility and monogermness, the female breeding pool went through a genetic bottleneck. Accordingly, breeders have systematically enlarged the female genepool by using their own breeding stock. Even though exotic germplasm was not used, after 30 years of broadening the female genepool, the genepool has sufficient variability. Today, breeders wish to broaden the whole breeding pool as such (female and male pools).

Strikingly, for sugarbeet breeders the crop itself still is the most important genetic resource used for the development of improved varieties today. One could argue that the genetic base of the crop as such is not as narrow as generally assumed. It seems rather that it is a lack of specific traits which hampers breeding progress. Indeed, because commercial plant breeders use a large number of different, heterozygous pollinator populations, hybrid varieties still have much genetic variation.

Additionally, sugarbeet is a wind-pollinated, strongly outcrossing crop. Therefore, plant breeders today may profit from exotic germplasm that was introgressed in the sugarbeet breeding pool, either by chance or deliberately by breeders. The first introductions of wild germplasm into sugarbeet probably occurred at the beginning of the 20th century, in Russia, the USA and Italy. Cultivated × wild beet crosses were, for example, described by Tjebbes (1933), who used *Beta vulgaris* ssp. *maritima* from the North Sea coast with a sugar content ranging from 15.7% to 17.6%; and Munerati (1932), who crossed a population from the Po estuary with sugarbeets to introduce genetic variation for resistance to *Cercospora beticola*. The Munerati material, at least, has been widely used in sugarbeet breeding.

Probably because of these early experiences with wild beet crosses, in the 1970s and early 1980s there was a great fear that introgression of undesirable genes of wild or

exotic germplasm along with the desired disease resistance trait would destroy the results of costly selection on high sugar quality and bolting resistance. However, the view on potential benefits arising from the utilization of exotic germplasm began to change when soil-borne diseases such as the beet cyst nematode (*Heterodera schachtii*) (Hellinga, 1943) or the beet necrotic yellow vein virus (BNYVV) (Grünewald *et al.*, 1983), already identified as very harmful disease agents in sugarbeet fields, began to spread and threaten the sugarbeet production in the whole northern hemisphere. Though many lines were tested, no major disease resistance genes against these important pests and diseases were detected in the crop. In addition, the level of tolerance to the cyst nematode proved to be insufficient in the breeding genepool (Curtis, 1970; Heijbroek, 1977). Interestingly, in some Italian varieties (cv. 'Roxane', 'Java', 'Alba'), there was some resistance or tolerance in an agronomically satisfactory genetic background. It is assumed that Italian varieties still contained some wild genes originating from the Munerati material. These sources have been used to develop the first varieties with Rizomania tolerance/resistance (Desprez and Desprez, 1999).

In 1956 Savitsky (1960) detected strong *Heterodera schachtii* resistance genes in *Beta* section *Procumbentes*. However, due to strong crossing barriers between section *Beta* and section *Procumbentes*, the utilization of this source proved to be very difficult and time-consuming. It is easy to understand that this specific experience did little to promote a broader use of exotic material in breeding programmes (Desprez and Desprez, 1996).

In the 1980s, the continued collecting and evaluation efforts of the USDA/ARS programme yielded more and more exciting results on new sources of resistances, for example to the Rizomania disease (Doney and Whitney, 1990) in *B. vulgaris* ssp. *maritima,* which crosses easily with sugarbeet. Since then, the interest in utilization of *Beta* genetic resource collections has been increasing worldwide. Breeders are mainly searching for disease resistance genes in exotic germplasm to supplement their breeding pool. The introduction of additional genetic variation for sugar content and yield genes from exotic germplasm is thereby welcomed as a positive side effect that can benefit breeding progress in the long run.

The Sugarbeet Breeding Research Community

Because of the small number of remaining large sugarbeet seed companies, collaboration between experts is no longer restricted to national projects. In the non-competitive sector particularly, there is a strong willingness to cooperate at international level. Knowledge as well as germplasm is exchanged across the northern hemisphere where sugarbeets are mainly produced. Pre-selected wild material from Europe can be found in Chinese breeding gardens, and Chinese leaf beets in European evaluation programmes. Due to the exchange of scientists between universities and the fusion of breeding companies at international level, national projects are becoming more and more an integral part of international activities. The different partners can be grouped as follows:

- Institutes and companies in Europe and the USA, with a strong interest in novel genetic variation for pest and disease resistance, drought and salt tolerance, which are

required to develop varieties meeting the demand for an ecologically sound sugarbeet production.

- Governmental institutes developing varieties (China, India, Iran, Poland, Ukraine, Bulgaria), with interest in access to high-yielding, high-quality breeding material, resistant germplasm and high-temperature tolerance.

Sugarbeet breeders and researchers from the commercial and public sector convene in different associations. The Study Group 'Genetics and Breeding' of the International Institute of Sugarbeet Research (IIRB) meets once a year and organizes joint research projects at international level that interest all breeding companies. Another international forum with a wide coverage of nationalities and scientific disciplines is provided by the World *Beta* Network (WBN). WBN meetings take place every 3 years and deal with joint activities for genetic resources conservation, documentation and utilization. Smaller, but nevertheless very important groups are the USDA/ARS Sugarbeet Crop Advisory Committee (annual meetings), other similar national associations and the French *Beta* Network which can also cooperate with partners outside the country. Discussion on the utilization of *Beta* genetic resources collections has become a permanent topic on the agenda of all these groups.

The Genus *Beta* and its Useful Characters

The genus, which is the raw material for breeders, consists of four sections, which can be grouped into three genepools (Table 17.1).

Breeders have successfully tapped the primary and tertiary genepools, while only a few attempts were made to use the secondary genepool. There are a number of reasons for this. Allthough stronger crossing barriers exist between section *Corollinae* and section *Beta* than between species within section *Beta*, interspecific hybrids can be produced. First attempts to introgress yellowing virus resistance from the *Corollinae* section into the sugarbeet (Dalke cited in Jassem, 1985) failed probably because of lack of sufficient chromosome homology between the *Corollinae* and the sugarbeet chromosomes, which is a prerequisite for crossing-over and recombination. In addition, while breeders were still engaged in the introgression of the nematode resistance genes from section *Procumbentes* into the sugarbeet, large-scale screening of the *B. vulgaris* ssp. *vulgaris* and ssp. *maritima* germplasm yielded donors of interest to breeders. For the time being there is therefore no real pressure for an urgent utilization of the secondary genepool. A third reason is lack of evaluation of the *Corollinae* section due to a practical problem arising from the fact that all *Corollinae* species are hard seeded. Thus, the pericarp cap has to be removed manually to facilitate germination, which is very time-consuming and has deterred investigators from large-scale screening. Section *Nanae* (*B. nana*) has never been taken into consideration for base-broadening projects. As a species adapted to high altitudes it is very difficult to handle at locations where sugarbeet breeding work is generally conducted. It is not known whether this species has ever been successfully multiplied *ex situ*, not to mention successfully grown for evaluation purposes.

All three genepools contain useful as well as undesirable wild characters (Dale *et al.*, 1985; Van Geyt *et al.*, 1990; Lewellen, 1992; Paul *et al.*, 1992; Stanescu, 1994; Büttner *et al.*, 1997; Mesbah *et al.*, 1997; Yu, 1997; Bosemark, 1998; Michalik *et al.*, 1998; Panella, 1998). Examples are provided in Table 17.2.

Table 17.1. Taxonomy of the genus *Beta*.

Primary genepool	Section *Beta* syn. *Vulgares* Ulbrich
	B. vulgaris L.
	ssp. *vulgaris* (cultivated beets)
	Leaf beet group
	Garden beet group
	Fodder beet group
	Sugarbeet group
	ssp. *maritima* (L.) Arcang.
	ssp. *adanensis* (Pamuk.) Ford-Lloyd & Will.
	B. macrocarpa Guss.
	B. patula Ait.
Secondary genepool	Section *Corollinae* Ulbrich
	Base species
	B. corolliflora Zosimovich
	B. macrorrhiza Steven
	B. lomatogona Fisch & Meyer
	Hybrid species
	B. intermedia Bunge
	B. trigyna Wald. & Kid.
	Section *Nanae* Ulbrich
	B. nana Boiss. & Heldr.
Tertiary genepool	Section *Procumbentes* Ulbrich syn. *Patellares*
	B. procumbens Smith
	B. webbiana Moq.
	B. patellaris Moq.

Bottlenecks to the Utilization of *Beta* Genetic Resources

The utilization of *Beta* genetic resources is confronted by several different kinds of problems. Accordingly, different strategies and methods have been developed for the introduction of new genetic material into the sugarbeet breeding pool.

The first problem is the fear of breeders that introgression of wild beet germplasm would require excessively high investments to recover the root shape, root yield, sugar yield and sugar quality of the cultivated parents. Hence, breeders tend to search in the sugarbeet breeding genepool first – sometimes in vain as in the case of resistance to *Heterodera schachtii*. O. Bosemark, head breeder of a Swedish company, was the first to say that this fear had no rational basis (Bosemark, 1989). In fact, the discussion initiated by Bosemark helped to promote the breeding approaches of researchers like Munerati (1932). Bosemark demonstrated in selection experiments that after crossing exotic material with sugarbeet, only a few selection cycles are required to regain a reasonable yield and root shape. In view of the narrow genetic base of the crop, he considered the potential profit for a breeder higher than the loss of funds arising from selection against wild characters in cross progenies of cultivated × exotic crosses.

Annual, quick-bolting wild types of section *Beta* form the second problem. The

Table 17.2. Characters relevant to beet breeding and their distribution over species.

Trait	Taxon code																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Annual life cycle	■	■	■	■	■	■	■	■	■									
Monogerm seed balls					■							■			■			
Hard seededness										■	■							
Seed shattering						■												■
CMS	■																	
Genic male sterility					■			■										
Salt tolerance						■												
Frost tolerance														■				
Curly top					■					■	■					■		■
Yellowing viruses						■						■	■	■				
Beet mosaic virus						■				■		■		■				■
BNYV virus						■												
Yellow wilt		■				■												
Peronospora farinosa				■														■
Erysiphe betae																		■
Rhizoctonia solani			■															
Cercospora beticola													■					■
Polymyxa betae												■						
Black leg disease			■	■														
Erwinia ssp.																■		■
Heterodera schachtii						■												
Heterodera trifolii						■												
Meloidogyne hapla						■										■		
Myzus persicae						■				■								
Pegomya ssp.														■				■

Taxon codes used: (1) *B. vulgaris* ssp. *vulgaris*; (2) *B. vulgaris* ssp. *vulgaris* leaf beet group; (3) garden beet group; (4) fodder beet group; (5) sugarbeet group; (6) *B. vulgaris* ssp. *maritima*; (7) ssp. *adanensis*; (8) *B. macrocarpa*; (9) *B. patula*; (10) *B. corolliflora*; (11) *B. macrorrhiza*; (12) *B. lomatogona*; (13) *B. intermedia*; (14) *B. trigyna*; (15) *B. nana*; (16) *B. procumbens*; (17) *B. webbiana*; (18) *B. patellaris*. ■ = variation detected.

evaluation for disease resistance is sometimes difficult to realize directly on such annual types and even if a useful trait is detected it is not always transferable to the crop as it may not be expressed in the genetic background of cultivated material. Because of these difficulties it has been suggested that annual wild types are first crossed with cultivated germplasm and the resulting biennial material is then screened. In the case of the leaf spot disease, for example, early-bolting plants cannot be evaluated precisely in the field test, while greenhouse and laboratory tests have a low correlation with field results (W. Mechelke, KWS, personal communication). Screening in the field is equally difficult because plants are already senescent when the disease develops. In the case of the *Cercospora beticola* leaf spot disease, it is then very difficult or even impossible to score. Similar difficulties are known for various other diseases. In addition, annual types when

tested in the field may contaminate the soil with seeds and contribute thereby to the weed beet problem.

The third problem arises from crossing barriers between section *Beta* and sections *Corollinae*, *Nanae* and *Procumbentes*, respectively (Jassem, 1992). They are particularly strong in the case of *Procumbentes* species. However, section *Corollinae* and *Procumbentes* contain characters that have not yet been detected in section *Beta*, such as insect resistance. Stanescu (1994) noted that *B. corolliflora* may be resistant to attack by *Mamestra brassicae* L. and *Noctuide loxostege stricticalis* L. larvae. Only few accessions of these hard-seeded species have been evaluated today. Breeders will perhaps one day find strong resistance genes acting against *C. beticola* in the secondary genepool.

Breeding Approaches to Broaden the Genetic Base of *Beta*

The different breeding programmes which have been developed to overcome these difficulties can be grouped in two categories:

1. In previous years, breeders only concentrated on the introgression (Simmonds, 1993; Spoor and Simmonds, Chapter 3, this volume) of desirable traits into the sugarbeet crop as fast as possible. 'Fast' can mean a few years as in the case of the primary genepool or more than a decade, as in the case of the tertiary genepool (see examples below).
2. Today, breeders have also started programmes that do not concentrate on a specific character but aim at broadening the genetic base of the crop in general. This type of approach has been described by Simmonds (1993; see also Spoor and Simmonds, Chapter 3, this volume) as 'incorporation'. Two examples are given below for incorporation from the primary genepool.

Introgression from the primary genepool

Examples of conventional breeding approaches are described by Desprez and Desprez (1999) and in more detail by Büttner *et al.* (1997). The BGRC 54817 (RNR 870909) held by the BAZ Genebank and collected in Normandy, France by Dutch scientists in 1970 showed variation for Rizomania resistance. Through selection of resistant single plants, followed by selfing and selection of resistant plants in the S_1-line, the character 'Rizomania resistance' could be fixed. A parallel backcross programme was started for inheritance studies and for broadening the genetic base of Rizomania resistance in sugarbeets. Büttner *et al.* (1997) applied a well-known breeding method, which is very successful if the donor parent crosses easily with the sugarbeet and if the character is simply inherited.

Introgression from the tertiary genepool

Strong crossing barriers exist between the *Procumbentes* species (*B. procumbens, B. webbiana* and *B. patellaris*) and the section *Beta*. Phylogenetic research using DNA

fingerprinting (Jung *et al.*, 1993) even suggests that the section *Procumbentes* could be considered as a separate genus. Recent results presented by Shen *et al.* (1997) also suggest that the section *Procumbentes* diverged from the other *Beta* species at a rather early evolutionary stage. This explains why introgression of resistance genes against the cyst nematode *Heterodera schachtii* into sugarbeet has been so difficult and time-consuming. Savitsky (1960) was the first who crossed *B. vulgaris* with nematode-resistant *B. procumbens*. In Germany, crosses between cultivated forms and the wild species *B. procumbens*, *B. webbiana* and *B. patellaris* were done by Löptien (1984) at the University of Hanover. Today, the resulting varieties are mainly used to decrease the nematode population density in infested fields. The first steps were production of alien monosomic resistant addition lines; the second step was production of diploid sugarbeet translocation lines carrying a small fragment of the wild chromosome with the resistance gene; the third step was genetic localization of the gene(s), cloning and sequencing of the nematode resistance gene $Hs1^{pro-1}$, and testing of the function of $Hs1^{pro-1}$ in transformation experiments (Cai *et al.*, 1997; Jung, 1997). By means of genetically transformed sugarbeet an important disadvantage of the conventionally developed nematode-resistant varieties – insufficient agronomic performance – may be overcome.

The nematode resistance gene originating from *B. procumbens* encodes a 282-amino acid protein, which has features quite similar to disease resistance genes previously cloned from other higher plants. This gene is not only useful for sugarbeet resistance breeding, but may also be of interest to breeding programmes outside the genus *Beta*, such as rapeseed (Jung, 1997).

Incorporation from the primary genepool

Colleagues from the USDA/ARS started a systematic sugarbeet enhancement programme in 1986. Crosses with wild *B. vulgaris* germplasm were made in 1986, 1990 and 1994. In 1990, male-sterile sugarbeet plants were chosen as the female parent to obtain F_1 plants. F_1 plants of each cross were intercrossed to produce F_2-families, which were then bulked to produce F_3 families. At least two recombination cycles were allowed before mild selection on root shape and bolting resistance was started. After five cycles of mass selection some of the progenies started to resemble sugarbeet. In this case no prior selection on useful characters was done. Testing on disease resistance followed later. Our USDA colleagues are very satisfied with this programme, which has steadily started to produce USDA germplasm releases (Doney, 1998; Panella, 1998). When officially registered by the *Journal of Crop Science*, the releases can be used by any breeder and fed into elite breeding programmes.

French colleagues have recently started a similar but more sophisticated breeding programme. It was launched by the company Florimond Desprez at the request of the Bureau des Ressources Génétiques (BRG). Almost all European breeding companies actively participate in this programme, which uses wild material of French origin. One of the interesting features is that the 'value' of the wild sources is only partly known. Wild material from Corsica, for example, contains variation for Rizomania resistance. Yet, no selection on this specific character is done before crossing. The difference compared with the introgression work done by Büttner *et al.* (1997) is the long-term

strategy behind it. It is a declared aim of the project: (i) to allow maximum recombination between the cultivated and wild sources; and (ii) to keep a half-and-half 'equilibrium' of the wild and cultivated genome (Doggett and Eberhard, 1968). For that purpose, so-called Doggett populations containing the alleles '*MM*' for multigermicity, '*aa*' for genetic male sterility, and the S_f allele for self-fertility are used as female parents (Owen, 1942, 1954). Crosses between $MMaaS_fS_f$ and wild *Beta vulgaris* ssp. *maritima* populations were made in 1996. The presence of the *aa*-allele allows the identification of male sterile plants in the population. Seeds are harvested on male-sterile plants only, which ensures maximum outcrossing and recombination. The programme is designed in such a way that each participant receives two French wild beet populations and produces two 'buffer' populations. It was agreed to exchange seed samples of the two progenies amongst the 11 participants in 1999 when the pre-competitive character of the programme ended. At that stage each partner owned pools originating from 22 different French wild beet populations. Subsequently, selection started for agronomic characters (especially root shape) and with the introduction of selfing cycles to produce inbred lines and crossing cycles to recombine the different sub-populations. Though sugarbeets are self-incompatible, the production of inbred lines is possible because of the presence of the S_f allele in each population. How to exploit this genetically broad material, which will get adapted to the environmental conditions prevailing at each selection site, is now at the discretion of each partner. This differentiation process will also contribute to a diversification of the elite breeding pool amongst companies and breeding institutions. A simplified description of the base-broadening programme is given in Scheme 17.1.

The activities of the French *Beta* Network follow similar principles as described by Mitteau (1997) for bread wheat and barley. The *Beta* programme allows collaborative projects on genetic resources management since the common material has no property rights on it. This is also an open programme so that any new participant can enter by contributing two new populations which can then be shared with the already participating partners without much disturbance. New participants, however, need to contribute actively to the network programme before they can profit from the work done by the others. In the long run it will produce material that could become useful for many international cooperative studies.

Incorporation from the secondary genepool

A fraction of the *Corollinae* material that is used in a research programme at the University of Kiel (Germany) was collected by a German scientist in Turkey in the 1970s. The Genebank of the Federal Centre for Breeding Research on Cultivated Plants (BAZ) maintains this material and has provided the Chinese University at Harbin in northeast China with *Corollinae* accessions. The aim of the project is the establishment of a set of alien monosomic addition lines, which were developed by the Chinese counterpart using *Corollinae* accessions.[1] The actual value of the *Corollinae* sources is not known, and it will be determined only after all theoretically possible alien

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[1] See http://www.plantbreeding.uni-kiel.de July 1998; personal communication of Professor C. Jung.

Scheme 17.1. Production of a buffer population using wild *Beta* from France.

Step 1: Production of F_1 seeds.

Year	Generation	Doggett population (DP) genotypes	Female parent (DP)	Wild population (WP) genotypes	Male parent (WP)	Explanation of the breeding step
1	F_0	1/2 *Aa*; 1/2 *aa* 1 *MM* 1 $S_1 S_1$ 1 *bb*	Sugarbeet	1 *AA* 1 *MM* 1 *S/ ?* 1 *B/ ?*	Seabeet	Production of sugarbeet and seabeet stecklings (= small beets cultivated for seed production, only)
2	F_0	1 *aa*	Sugarbeet	1 *AA*	Seabeet	Before flowering *Aa* sugarbeet genotypes are discarded. Seabeet plants pollinate male-sterile sugarbeet plants. Seeds are harvested on *aa* sugarbeet genotypes separately (half-sibs). Seeds of the seabeet population are harvested as a bulk to maintain the original accession.

Explanations of genotypes: *AA* = genic male-fertile; *aa* = genic male-sterile type; *MM* = multigerm; *mm* = monogerm type; $S_f S_f$ = self-fertile type; $S_{1-n}/$? segregating self-incompatible, sterile type, S_f is dominant to all alleles of the S-series; *BB* = annual, *bb* = biennial type, *B/?* = segregating annual type .

Step 2: Production of the F_3 generation starting from F_1 seeds.

Year	Generation	Male-fertile (*AA*, *Aa*) /sterile (*aa*) genotypes	Explanation of the breeding step
2	F_1	1 *Aa*	Sowing of separately harvested half-sib families. The genome consists of 50% sugarbeet and 50% seabeet genes.
3	F_1	1 *Aa*	Singling of F_1 plants to an equal field stand per half-sib family to ensure about equal genetic contributions of each of half-sib family to the F_2. The F_2 seed sample is harvested on each half-sib family separately.
3	F_2	1/4 *AA*, 1/2 *Aa*, 1/4 *aa*	Sowing of half-sib families to produce F_2 stecklings.
4	F_2	1/4 *AA*, 1/2 *Aa*, 1/4 *aa*	All *aa* genotypes are earmarked at flowering and seeds are harvested only on *aa* genotypes.
4	F_3	2/3 *Aa*, 1/3 *aa*	Mailing of F_3 seed samples to each participant. Mutual exchange of F_3 seed material.

Step 3: Production of the buffer population.

Year	Generation	Male-fertile (AA, Aa) /sterile (aa) genotypes	Explanation of the breeding step
4	F_3	2/3 Aa, 1/3 aa	Sowing of the separately harvested half-sib families derived from an individual sugarbeet × seabeet accession cross DP × $WP_{1...n}$ to produce aa genotypes of this specific F_3. Other F_3 families produced by programme partners are sown accordingly.
5	F_3	2/3 Aa, 1/3 aa	Depending on the number (k) of F_3s within a particular $DP \times WP$ cross exchanged between participants, a maximum of $n \times k$ half-sib families will jointly flower and intercross. Seeds are again harvested on aa genotypes, only. Within each $DP \times WP_{1...n}$ family, aa genotypes can be harvested as a bulk.
5	F_4	1/2 Aa, 1/2 aa	The Doggett population is at gene equilibrium. The individual $DP \times WP_{1...n}$ should be kept separately during the next generations of intercrossing. Plants still contain about 50% sugarbeet and 50% seabeet genome.
6	F_4	1/2 Aa, 1/2 aa	Sowing of $n \times (DP \times WP)$ families for mild mass selection on agronomic characters such as root shape and bolting resistance. Production of inbred lines, if considered to be already useful, is possible through the segregating S_f allele.

WP_1 = wild population no. 1; WP_2 = wild population no. 2; etc.

▢ = generative phase.

monosomic addition lines have been established. By testing these addition lines for disease resistance, the researchers will try to localize resistance genes on the wild beet chromosomes. After backcrossing with sugarbeet, diploid, resistant recombinants can perhaps be selected as basic material for breeding. This approach has a basic similarity to the French Doggett population concept: the specific value of the wild *Corollinae* parent is not known precisely.

Future Role of Genebanks in Germplasm Enhancement Programme

As a consequence of the long-term base-broadening programmes initiated in the USA and France, considerable fractions of genetic diversity will be maintained in buffer populations. Genebank accessions which were used to create these buffer populations are further maintained as individual accessions in genebanks. Hence, genetic diversity stored in genebanks will become duplicated in base-broadening programmes. Today, our *Beta* collections are static. Genebank managers keep nicely classified and documented seed samples in their stores. In future, at least in the case of outcrossing species, genebanks could assume new functions. Besides the maintenance of rationalized static collections, genebanks could become responsible for the maintenance of more dynamically managed genepools resulting from different kinds of programmes. In an outcrossing crop, the role of a genebank manager may become more that of a genepool manager, coordinating and linking: (i) *in situ* maintenance of natural populations; and (ii) sampling and *ex situ* conservation of populations; with (iii) base-broadening work.

Base-broadening work can last for a long period aiming at the creation of new diversity through continued recombination and evolution. Since genebanks already have long-term responsibilities, these institutions may be in a good position to follow long-term germplasm maintenance and breeding strategies.

In France, native *B. vulgaris* ssp. *maritima* populations are already managed *in situ* in their natural environment, which enables seed harvest on request for evaluation purposes, and helps to avoid multiplication and storage of accessions in an *ex situ* collection. In addition, by grouping a number of wild populations of similar origin, the French base-broadening programme decreases the number of accessions that need to be manipulated. Furthermore, better adapted, dynamically managed material is of higher interest to breeders.

In the field of base-broadening, genebanks could:

- Run simple selection projects that are required to adapt wild germplasm to routine screening methods, as in the case of annual wild *Beta vulgaris*.
- Maintain buffer populations in the deep-freeze store if there is a temporary lack of funds required for continuation of the work, or if populations have fulfilled their current purpose.
- Maintain information on the purpose and breeding history of buffer populations for future users.
- Maintain donor lines with high frequencies of useful genes, as has already been briefly described by Büttner *et al.* (1997).

Natural evolution, as well as breeding, is a dynamic process. An integrated germplasm conservation and utilization programme linking *in situ* maintenance, *ex situ*

conservation and base-broadening can therefore better mediate between evolution and breeding than static genebank collections. It is at least our impression that the integration of these three elements of germplasm conservation and utilization has made considerable progress in sugarbeet in recent years.

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