Chapter 6
Sugar Beet

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1 Introduction

World sugar production is around 160 Mt yearly with a per capita consumption of about 23 kg. Total utilization is increasing approximately 1.4% annually thanks to the improved standard of living in densely populated countries like China and India. About one-quarter of world production is extracted from beets (*Beta vulgaris* L. ssp. *vulgaris*), and the remainder from cane (*Saccharum officinarum* L.). The chemical composition of both commercial sugars is sucrose (more than 99.5% in white crystalline sugar) despite the crops being very different in their climatic requirements and photosynthetic pathways. Beets yield better in temperate climates, especially in areas such as France, Germany, northern USA, whereas cane requires a tropical to subtropical environment (India, Australia, Cuba, Brazil, etc.). Sugar from beet and cane has completed in the market place since the earliest sugar beet factories produced sugar in the early 1800s. One advantage cane processing enjoys, among other things, is that cane factories can be energy sufficient due to the burning of bagasse (fibrous matter remaining after crushing the cane stalks), whereas the power for processing beets generally relies on fossil fuels. The cost of cane sugar is currently lower and the price differential for sugar extracted from beets and from cane follows the price of crude oil.

2 Origin and Domestication

Sugar beet is classified *Beta vulgaris* L. ssp. *vulgaris* sugar beet group (Lange et al., 1999). The second ssp. is *Beta maritima* (L.) Arcang., classified by Linnaeus (1797) as a separate species. The genus *Beta* L., of the family *Amaranthaceae* (formerly *Chenopodiaceae*), is subdivided into four sections (Table 6.1). All cultivated beets are included in the sub-species *vulgaris* that belongs to the species *vulgaris* and to

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Table 6.1 Taxonomy of the genus *Beta* (Letschert, 1993; Ford-Lloyd, 2005)

	Genus *beta*		
	Section *Beta* (syn. *Vulgares* Ulbrich)		
2*x*, 3*x*, 4*x*[a]	*Beta vulgaris* L.	ssp. *vulgaris*	Leaf beet group[b] Garden beet group[c] Fodder beet group[d] Sugar beet group
2*x*, 4*x*	*Beta macrocarpa* Guss.	ssp. *maritima* (L.) Arcang.	
2*x*	*Beta patula* Ait	ssp. *adanensis* (Pamuk.) Ford -Ll. et Will.	
	Section *Corollinae* Ulbrich		
2*x*, 4*x*	*Beta lomatogona* Fisc. et May.		
2*x*	*Beta macrorhiza* Stev.		
4*x*	*Beta corolliflora* Zos. ex Buttler		
4*x*	*Beta intermedia* Bunge		
4*x*, 6*x*	*Beta trigyna* Waldst. et Kit.		
	Section *Nanae* Ulbrich		
2*x*	*Beta nana* Boiss. et Heldr.		
	Section *Procumbentes* Ulbrich (syn. *Patellares* Tranzschel)		
2*x*	*Beta procumbens* Sm.		
2*x*	*Beta webbiana* Moq.		
4*x*	*Beta patellaris* Moq.		

[a]Number of chromosomes ($2x = 18$; $3x = 27$; $4x = 36$; $6x = 72$).
[b]Also named Mangold, Spinach beet, Chard, Swiss chard etc.
[c]Also named red beet.
[d]Also named forage beet.

the section *Beta* (Letschert, 1993; Letschert et al., 1993; Lange et al., 1999; Ford-Lloyd, 2005). Wild beets (i.e., the species and sub-species (ssp.) of the genus *Beta* outside of *B. vulgaris* ssp. *vulgaris*) have only been used as potential sources of useful traits for cultivated beets, particularly disease resistance characters (Coons, 1975; Lewellen and Whitney, 1993; Asher et al., 2001). Artificial hybridizations between section *Beta* species and sections *Corollinae*, *Nanae*, and *Procumbentes* have proved very difficult (McGrath et al., 2007). Sea beet [*Beta vulgaris* L. ssp. *maritima* (L.) Arcang.] was domesticated pre-historically somewhere in the Middle East (Coons, 1949; 1954; Campbell, 1984). Because the wild species normally flowers 2–3 months after emergence, the first growers would likely have selected beets with delayed bolting and flowering. In this way, as for several vegetables, the growing season was extended under cultivation, with the leaves being used as food (Campbell, 1984; McGrath et al., 2007). Following a long period of mass selection, cultivated beets became predominantly biennial and entered their reproductive

phase after overwintered vernalization (Biancardi, 1984). About 1000 BC, leaf beet was grown in Greek Mediterranean countries and later spread through the Roman Empire where the crop was named *Beta* (von Lippmann, 1925). Here, a second cultural variant with expanded hypocotyl and root became an important vegetable. The precise origin of table beet (also named garden or red beet) is obscure. During the Middle Ages another cultural variant of beet, characterized by larger roots suitable for livestock fodder, was developed in northern Europe (Campbell, 1984).

After the discovery that fodder beets contained the same kind of sugar as cane, the fourth crop variant was selectively bred in Germany toward the end of the 1700s (Achard, 1803; Knapp, 1958). This selection led to the first sugar beet variety (Fischer, 1989), the "Weisse schlesische Rübe" (White Silesian Beet). Achard built the first beet sugar factory at Cunern (Silesia), which began operation in the spring of 1802 (Winner, 1984). After a few years of expansion, the crop acreage decreased quickly in favor of cane, due to changes in international trade. Beet cultivation and the construction of factories began again in Germany around 1830, partially because sugar beet culture improved greatly the yield of rotation crops (Coons, 1949).

During the early breeding efforts, sugar yield increased rapidly as the result of new analytical and breeding methods developed in France (McFarlane, 1971). Cultivation methods were improved with the employment of chemical fertilizers and steam tractors, which allowed deeper plowing and better soil management. In the twentieth century, improvement was characterized by continuous progress in breeding and agronomy leading to a reduction in growing costs and an increase of sugar yield (Robertson-Scott, 1911; Winner, 1993). The singling of seedlings was needed because the multigerm "seed" (fruit) sown was composed of two to five fused true seeds. Approximately 100 man-h/ha that had been required to thin and single stands to the desired population density was eliminated after the discovery of genetic monogermity (Savitsky, 1950). The adoption of monogerm seed greatly reduced hand labor and stimulated a rapid evolution of cultural practices. Pelleted seed with incorporated chemicals improved sowing precision and provided better protection against seedling diseases (Leach and Bainer, 1942; Winner, 1993). Sugar beet was one of the first crops protected with chemicals (arsenic, nicotine, sodium fluoride, sulfur, copper salts, etc.) and herbicides (Winner, 1993). The discovery of some genetic resistances to diseases increased sugar yield while reducing dependence upon pesticides. Approximately half of the improvement in sugar yield can be attributed to breeding (Sneep et al., 1979). The most important improvements over the last 50 years have been the introduction of hybrid varieties, the pest and disease resistances, including that to rhizomania and sugar beet cyst nematode, the meristem multiplication techniques, and breeding assisted by molecular biology (Biancardi et al., 2005). Thanks to integrated research efforts, the increase of sugar yield per hectare in advanced European countries is about 1.4% annually (Bosemark, 2006).

Sugar beet in the northern hemisphere is usually sown in late winter or early spring. Depending upon climatic and soil conditions, the crop is harvested after 5–9 months of growth. In Mediterranean climates, sowing may be in autumn (see Section 4.5) with spring/summer/fall harvest. Mechanically topped and lifted roots are either transported to the factory quickly or placed in storage piles, depending on the temperature and weather conditions and the throughput of the factory. The tops

(e.g. crowns, petioles, and leaves) are removed from the beet because of the low sugar content and the high concentration of processing impurities (see Section 5.1 and Fig. 6.5). After washing, sugar is extracted with hot water diffusion from thinly sliced roots. The "raw juice" is purified with repeated treatments of lime and carbon dioxide. After filtration, the "thin juice" is concentrated by evaporation. When sucrose concentration becomes greater than 60%, crystallization of sugar is initiated in "thick juice" under partial vacuum and high temperature conditions. Molasses, a brown and heavy syrup containing about 45% sugar, are separated from crystalline sucrose by centrifugation. Crystallized raw sugar undergoes further processing to obtain nearly pure, commercial, white sucrose (McGinnis, 1982). Molasses are used for animal feed and for production of alcohol, glutamate, yeasts, etc., or may be returned through the factory for further sugar removal and separation of sucrose by molecular sieving and ion exchange. The pulp, i.e., the non-soluble part of the sliced roots after sugar extraction, is used mainly for animal and pet food.

3 Genetic Resources

Although sugar beet is a relatively new agricultural crop and was not cultivated until the early 1800s, beet was domesticated as a leafy pot herb in pre-historical times (Ford-Lloyd et al., 1975; De Bock, 1986). It is thought that the gene pool of white fodder beet provided the genetic base for early sugar beet varieties. It has been suggested that this narrow germplasm base has left sugar beet with a narrower genetic pool than that of other open-pollinated crops (Bosemark, 1979; 1989; Lewellen, 1992). Because early sugar beet development and production was in the temperate climate of Northern Europe, which was relatively disease free, there was little pressure to select or maintain high levels of host-plant resistance (Lewellen, 1992). As sugar beet production moved out of Northern Europe into warmer zones, endemic diseases were encountered that severely limited yield and for which there were no known resistances (Lewellen, 1992). The first attempts to screen exotic and wild-beet germplasm at the beginning of the 1900s, primarily for disease resistance, were undertaken in response to this increasing pest and disease pressure.

One of the first successful attempts to use exotic germplasm was in the Po Valley of Italy in the early 1900s, where the high humidity and warm night temperatures provide optimal conditions for cercospora leaf spot (CLS) caused by the fungus *Cercospora beticola* Sacc. Here we find the first documented instance of collecting sea beet germplasm (*B. vulgaris* ssp. *maritima*) to use in a sugar beet breeding effort. Munerati et al. (1913) recognized the potential of the sea beet growing in the Po Delta as a source of host-plant resistance to CLS. The germplasm produced in this breeding program, the Rovigo series (R148, R581, etc.) and the varieties "Cesena" and "Mezzano," has been adopted worldwide and is the source of most CLS-resistant germplasm in use today (Munerati, 1932; Biancardi and De Biaggi, 1979).

In other countries of Europe, researchers studied sea beet and crossed it to sugar beet (Rasmussen, 1933; Tjebbes, 1933). There were other efforts to develop

CLS-resistant varieties as Munerati had done (Stehlik, 1949; Schlösser, 1957), and varieties with resistance to other diseases (Margara and Touvin, 1955, reviewed by Asher et al., 2001). However, it is difficult to estimate the extent to which sea beet germplasm was used in commercial breeding programs, especially because of undesirable traits that could potentially be introduced with its use, e.g., fangy roots, annualism, high fiber content in the root, elongated crowns, red pigment (in root, leaf or petiole), and lower sugar production [reviewed by Coons (1975) and by Panella and Lewellen (2005)].

Commercial sugar beet seed production was initiated in France around 1810 by the firm Vilmorin. About 10 years later breeding activities including mass selection (mother root selection) and progeny test selection (Oltmann, 1984) were begun. Vilmorin is credited with being the first to use progeny test methods for improvement of any crop. In Germany, the first firms active in sugar beet seed production were Ziemann (around 1830), Rimpau (around 1841), and Knauer (1849). Because of the strategic importance of seed supply for the sugar factories, numerous breeding and seed production centers were developed in nearly every country where sugar beet was cultivated. Due to the proprietary nature of this activity, the circulation and distribution of sugar beet germplasm in Europe became tightly controlled, as it remains today (Oltmann, 1984). For this reason, sugar beet breeding and germplasm conservation evolved differently to that in the United States and have been largely proprietary.

Until World War I, most sugar beet seed used in the United States came from Europe. The disruption of seed importation from Germany caused by the war led to the establishment of domestic seed production, and by the end of the 1930s, domestic production provided about one-third of the needs of the United States (Coons, 1936). USDA researcher, G.H. Coons, who was familiar with Munerati's work, made collection trips to Europe and Asia to look for sources of CLS, and curly top, resistances in sea beet (Coons et al., 1931) as well as in the other species in the genus *Beta* (Coons, 1975). USDA researchers in the United States made some effort to evaluate this material, and material collected by Stewart in 1969, for resistance to CLS (Bilgen et al., 1969), rhizoctonia root rot caused by *Rhizoctonia solani*, and black root caused by *Aphanomyces cochlioides* (Schneider and Gaskill, 1962). The germplasm was stored in Beltsville, MD, where storage conditions were poor, and what survived was taken by McFarlane to Salinas, CA, for regeneration. The part of the collection that was rescued (in the United States, 93 wild-beet accessions within the range WB1–WB319) was extensively evaluated and has provided genes for many useful traits (Whitney, 1989a, b; Lewellen and Whitney, 1993; Yu et al., 1999; Lewellen and Schrandt, 2001).

A number of changes in sugar beet breeding came together in the 1960s. This confluence caused a genetic bottleneck in this time period, which exacerbated growing disease pressure due to an increase in cultivated area and shortening of the rotation between sugar beet crops. These were the cytoplasmic male sterility (CMS) and genetic fertility restoration system developed by Owen (1954b) and the introduction of new monogerm, CMS and O-type maintainer lines to produce commercial monogerm, CMS hybrid varieties (Savitsky, 1950: McFarlane, 1971). Until

the 1980s, there seemed to be a reluctance to use wild-beet germplasm, perhaps because of earlier experiences that resulted in the introgression of many undesirable traits from the exotic germplasm (Frese et al., 2001). The need for increased resistance to disease and insect pests and a greater productivity rekindled interest in sea beet and other exotic sources of germplasm (Lewellen, 1992).

The Sugar Beet Crop Advisory Committee (now Crop Germplasm Committee-CGC) formed in 1983 represents the sugar beet germplasm user community in the United States. The sugar beet CGC is still an integral part of the USDA-ARS's National Plant Germplasm System (NPGS) (reviewed by Janick, 1989), as well as an official committee of the American Society of Sugar Beet Technologists (ASSBT). Since its inception, this committee has consisted of sugar beet seed industry members, plant breeders, university researchers, and USDA-ARS scientists. The sugar beet CGC has aggressively supported evaluation of the *Beta* germplasm within the USDA-ARS NPGS (Panella and Lewellen, 2007).

The increasing interest in wild germplasm as a genetic resource for improving sugar beet varieties heightened the realization that wild *Beta* germplasm was being lost in the 1980s and 1990s (Pignone, 1989; Doney et al., 1995). The value of the wild relatives in the improvement of the sugar beet crop was well demonstrated (De Bock, 1986; Doney and Whitney, 1990; van Geyt et al., 1990; Lewellen and Skoyen, 1991; Doney, 1993), and using evaluation data from the sugar beet CGC evaluations, the USDA/ARS public sugar beet breeders began introgressing wild germplasm into the sugar beet gene pool (Doney, 1998; Panella, 1998; Panella and Lewellen, 2007). This germplasm was released in the United States to sugar beet seed companies, as well as released internationally (Lewellen, 1991, 1997; 2000a, b; Yu, 2002). The Genetic Resources Information Network (GRIN) Database of NPGS *Beta* collection includes everything from wild relatives (Hannan et al., 2000; Panella et al., 2003) to heritage open-pollinated varieties (McGrath et al., 1999) and germplasm registered in Crop Science (Doney, 1995). Of the 2,550 *Beta* accessions in the NPGS, the 572 sea beet accessions are among the best characterized and evaluated as well as being among the most useful in breeding programs (Panella et al., 2003). As of 2003, about 25,000 evaluation records (descriptors multiplied by accessions evaluated) are in the database (Panella and Frese, 2003). These and other data in the GRIN database can be accessed through the URL: www.ars-grin.gov/npgs.

During the 1980s in Europe, sugar beet breeders were developing a theoretical framework for effectively introgressing new germplasm into elite breeding programs, which has been expanded into a strategy to broaden the germplasm base of the sugar beet gene pool (Bosemark, 1989; Frese, 1990). This prebreeding strategy has been implemented through the World *Beta* Network (WBN), founded in 1989 with the goal of improving international collaboration among users and curators of germplasm collections throughout the world (Frese, 1990). A central database of all *Beta* accessions contained in genebanks throughout the world, the International Data Base for *Beta* (IDBB), maintained at the Federal Centre for Breeding Research on Cultivated Plants (BAZ) Gene Bank (Quedlinburg, Germany), has been developed and supported by the WBN members.

Building on the WBN strategy, public and private plant breeders within the International Institute for Sugar Beet Research (IIRB, Brussels), Genetics and Breeding Group, started developing Doggett buffer populations improved through recurrent selection (Doggett and Eberhart, 1968; Bosemark, 1971). Additionally, Frese (2000) developed an international core collection comprising 805 accessions of the IDBB in various genebanks in Europe and around the world. The GENRES CT95 42 Project, funded through the European Union, evaluated between 300 and 700 accessions of the synthetic core collection for resistance to seedling diseases (caused by *A. cochlioides* and *Phoma betae*), leaf diseases (caused by *C. beticola, Erysiphe betae*, beet yellows virus, and beet mild yellowing virus), the root diseases rhizomania (caused by *beet necrotic yellow vein virus*), and rhizoctonia root and crown rot (caused by *R. solani*), as well as drought tolerance (Panella and Frese, 2003). Data from this project can be accessed and downloaded at the URL: http://ice.zadi.de/idbbonline/beta.php and users can query passport, characterization, and evaluation data (including statistical parameters) (Panella and Frese, 2003). Private and public plant breeders in Europe and throughout the world have taken the results of these evaluations and are beginning to introgress these newly discovered sources of disease resistance into sugar beet (Asher et al., 2001; Biancardi et al., 2002; Luterbacher et al., 2000; Panella and Lewellen, 2007).

4 Major Breeding Achievements

Breeding has obtained significant results in enhancing the yield traits and the genetic resistances against several diseases, in some cases allowing sugar beet to survive even where serious infections are otherwise uncontrollable. Here we look in more detail at a number of achievements which have affected breeding methods and the types of cultivar produced.

4.1 Polyploidy

Efforts to modify the number of chromosomes in sugar beet became successful after the discovery of the mutagenic properties of colchicine (Schwanitz, 1938). The first tetraploid families, having twice ($2n = 4x = 36$) the normal number of chromosomes ($2n = 2x = 18$), were characterized by better root shape and fewer but larger leaves with shorter and stronger petioles than diploid ($2x$) beets (Lasa and Romagosa, 1992). Flowers, seed clusters, and pollen grains were also larger. Seed germination and root development of tetraploid ($4x$) families (genotypes reproduced with open pollination) were, on average, slower compared to their $2x$ counterparts, and bolting resistance was slightly improved. The main disadvantages in selecting genotypes at $4x$ level were due to the slower breeding response and increased difficulties to introduce new traits (Bosemark, 2006).

The $2x$ and $4x$ families are easily crossed, producing triploid ($2n = 3x = 27$) hybrids, manifesting intermediate morphological characteristics. Triploid ($3x$)

Table 6.2 Production system of commercial varieties in chronological order of cultivation

Production systems			Year of introduction[a]	Varieties
Multigerm varieties				
2*x* F *MM*			1802	2*x*, *MM* open pollinated
2*x* F *MM* × 4*x* F *MM*			1951	2*x* + 3*x* + 4*x*, *MM* anisopliod open pollinated
4*x* F *MM*			1966	4*x*, *MM* open pollinated
Monogerm hybrid varieties				
Seed bearers		Pollinators		
2*x* CMS *MM*	×	2*x* F *MM*	1954	2*x*, *MM* top cross
2*x* CMS *MM*	×	4*x* F *MM*	1954	2*x*, *MM* top cross
2*x* CMS *mm* (line)	×	2*x* F *MM* (line)	1955	2*x*, *Mm*[b] single cross
2*x* CMS *mm* (line)	×	2*x* F *MM* (family)	1955	2*x*, *Mm* top cross
2*x* CMS *mm* (F1)	×	2*x* F *MM* (family/line)	1955	2*x*, *Mm* three-way cross
2*x* CMS *mm* (F1)	×	2*x* F *MM* (F1)	1957	2*x*, *Mm* double cross
2*x* CMS *mm* (line)	×	4*x* F *MM* (line)	1959	3*x*, *Mm* single cross
2*x* CMS *mm* (line)	×	4*x* F *MM* (family)	1959	3*x*, *Mm* top cross
2*x* CMS *mm* (F1)	×	4*x* F *MM* (family/line)	1965	3*x*, *Mm* three-way cross
2*x* CMS *mm* (F1)	×	4x F *MM* (F1)	1965	3*x*, *Mm* double cross
4*x* CMS *mm* (line)	×	2*x* F *MM* (family/line)	1974	3*x*, "reverse" *Mm* top cross or single cross
4*x* CMS *mm* (line)	×	4*x* F *MM* (family/line)	[c]	4*x*, *Mm* top cross or single cross

F, male fertile; CMS, male sterile; *mm*, monogerm; *Mm* and *MM*, multigerm.
[a]According to Sneep et al. (1979).
[b]Phenotypichally monogerm because harvested on monogerm plants.
[c]Not released.

hybrids display better sugar yield than their parental averages, indicating heterosis. This important advantage was used for the production of anisoploid varieties. The seed was obtained by crossing 2*x* and 4*x* families transplanted in a 1:3 ratio. The higher proportion of 4*x* plants compensated for the lower competitiveness of their pollen. The bulk harvested seed had a percentage of 3*x* hybrid plants as high as 50%, thus ensuring a superior sugar yield (McFarlane, 1971; Sneep et al., 1979). The remaining seed comprised various proportions of 2*x* and 4*x*. Anisoploid varieties were widely used after 1951 (Table 6.2).

4.2 Monogerm Seed

The flowers in the section *Beta* are joined in clusters of two or more, which develop multigerm "seed," botanically classified as utricle and formed by the aggregation of as many fruits each containing the true seed (Klotz, 2005). After emergence, manual thinning was necessary not only to avoid competition among the plantlets emanating from the multigerm seed, but also to achieve a regular stand of about

80,000–100,000 equally spaced plants per hectare. Since hand thinning was very expensive, mechanically processing multigerm glomerules into single seeds was used (Fig. 6.1) (Knapp, 1958). Sowing with precision machines the "monogerm" seed obtained in this way, the requirement for hand thinning was strongly reduced, but not eliminated. In fact, the complete removal of bigerm seeds was difficult when using the gravity separators widely used during seed processing.

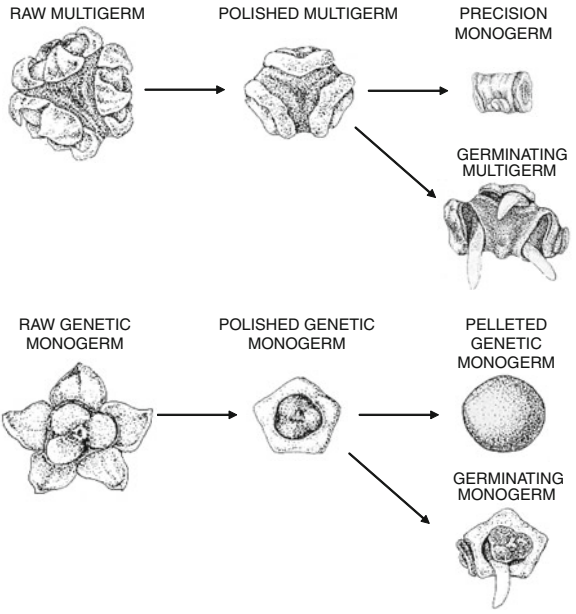


Fig. 6.1 Processing steps of multigerm/precision seed (*above*) and genetic monogerm seed (*below*) (from Biancardi, 1984, modified)

In 1948, plants with single flowers developing monogerm seeds were discovered and deployed (Savitsky, 1950). The first genetic monogerm germplasm, SLC 101, was available in 1951, and the commercialization of monogerm varieties was initiated some years later (McFarlane, 1971). Currently, only genetic monogerm varieties are in use, except in countries where the field emergence is difficult and/or labor costs are still low, such as in Northern Africa and China. The monogerm character depends on a pair of alleles designated *Mm* and it is in homozygous recessive condition. Other forms of monogermy have not been used commercially to date (Brewbaker et al., 1946; Shavrukov, 2000).

4.3 Male Sterility

Commercialization of hybrids became possible in 1955 (Sneep et al., 1979), after the discovery of genetic-cytoplasmic male sterility (CMS) by Owen (1945). The existence of a sterile cytoplasm (S) was demonstrated, resulting in sterility only in presence of two pair of alleles, designated *Xx* and *Zz*, in a homozygous recessive condition. Therefore, the CMS lines must possess the S *xxzz* genotype, whereas

all other combinations produce fertile or partially fertile offspring. The normal (N) cytoplasm always produces fertile progeny. The reproduction of CMS lines required the employment of maintainers bearing the N cytoplasm and the genes *x* and *z* in homozygous recessive condition. The maintainers, to which the monogerm character was soon transferred, were called O-types (McFarlane, 1971). At the beginning, both CMS and monogerm inbred lines (genotypes reproduced with more or less strict self-pollination) were very weak, but after crossing vigor and the seed production improved slightly (McFarlane, 1971). For reproduction, each CMS line needs a corresponding O-type. At least six to eight backcrosses are needed to create similar genotypes differing predominantly by their N- and S-cytoplasms (Fig. 6.2) (Sneep et al., 1979; Skaracis and De Biaggi, 2005). Nuclear (also named genetic or Mendelian) male sterility (NMS) depends on alleles at the locus *Aa* and is expressed in homozygous recessive condition (Owen, 1952). In contrast to CMS, NMS is not suited for commercial hybrid seed production, and consequently its use is limited to some specialized breeding schemes (Bosemark, 1971).

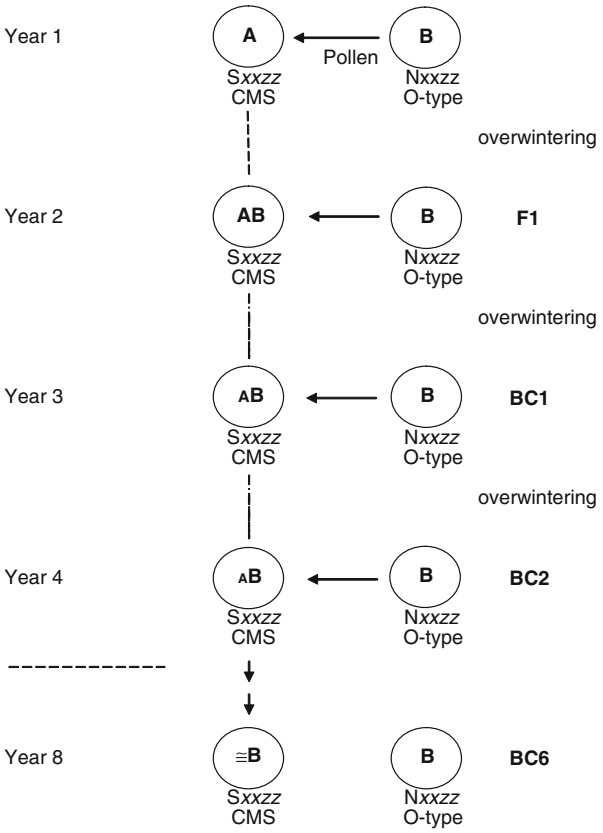


Fig. 6.2 Backcrossing for conversion of O-types to CMS maintainers

4.4 Growth Habit

The cultivated beets are biennial, that is, they require a vernalization period (overwintering) to begin the reproductive phase (Letschert et al., 1993). Under certain weather conditions (cold and increasing day length), biennial beets may vernalize in the field, giving rise to bolting plants (Fig. 6.3), and releasing fertile pollen and producing viable seed (Smit, 1983). Since seed production in Europe takes place in regions where annual beets are quite common, conditioned by alleles at the *Bb* locus where the recessive state confers biennial habit, pollen from annual plants transmits the bolting tendency and can be particularly damaging in seed production areas. The seeds shed from bolting sugar beets in the field pollinated with pollen from annual beet develop as annual beets, also named weed beets (Letschert et al., 1993), causing weedy infestations often difficult to control in subsequent beet crops. Weed beets flower like the wild ones a few months after emergence. The annuality trait depends on the dominant gene *B* (Munerati, 1931; Owen, 1954a). Bolting and flowering in annual genotypes occurs without influence of temperature or day length (Abegg, 1936; Abe et al., 1997).

4.5 Bolting Resistance

Usually a small proportion (around 0.1%) of beets in commercial fields bolts and flowers. High temperatures after the bolting induction may reverse its effects

Fig. 6.3 Bolted beet in field condition

(devernalization) (Smit, 1983). Notwithstanding the complexity of flowering physiology in biennial beets and genotype × environment interactions, selection has improved bolting resistance. Early sowing is effective in inducing bolting as a breeding tool for mass selection. Since early sowing in field conditions is not always possible, different greenhouse systems with combined photo-thermal treatments were developed. Bolting resistance is perhaps best accomplished using progeny testing (McFarlane, 1971). Due to the strong genotype × environment interactions, achieving significant progress in bolting resistance is only possible by selecting in the local climate where the improved variety will be grown (Smit, 1983).

The use of bolting resistant spring varieties enabled earlier drilling, resulting in a longer growth period and in a slightly improved sugar yield. Varieties endowed with a high degree of bolting resistance are also used for autumnal sowing in areas where a mild climate allows the overwintering of the crop (California, southern Spain, southern Italy, North Africa, etc.). Extending autumn sowing northward has good potential to increase sugar yields, but seems quite difficult due to the limited possibilities to significantly improve cold and bolting resistance. The former trait is needed by plantlets to survive winter; the latter is necessary for reducing the effects of intense bolting induction. Among other things, such enhanced bolting resistance would hinder the flowering when seed production is necessary (Smit, 1983). Because bolting of winter beets in cold areas can be as much as 100%, beginning in April, the large biomass yield (roots, leaves, and seed stalks) could be employed for fermentation and biogas production (Kluge-Severin et al., 2009).

Bolting resistance is likely controlled by several genes acting through different mechanisms, but the precise genetics are yet undetermined (McFarlane et al., 1948; Le Cochec, 1989; Jolliffe, 1990; Sadeghian and Johansson, 1993).

4.6 Self-Sterility and Self-Fertility

Sugar beet is primarily self-sterile (or self-incompatible). Self-pollination is quite rare in wild beets. Self-sterility was employed to enhance and maintain the heterosis in multigerm varieties before the discovery of CMS (Owen, 1942). The self-sterility trait generally acts through hindering the growth of the pollen tubes inside the pistils (Savitsky, 1950). According to Owen (1942), self-sterility is explained by multiple alleles S^1–S^n and Z^1–Z^n. The hypothesis assumed that a single *S* or *Z* factor carried by the pollen, if not present in the tissue of the stigma, causes fertility. A second model considers gametophytic self-incompatibility conditioned by four *S* loci with complementary interactions. The *S* genes in the pollen encountering the same allele(s) in the pistil result in incompatibility (Larsen, 1977, 1978).

The release of the first monogerm lines, which were also self-fertile, lead to the introduction of the trait into commercial germplasm (Savitsky, 1950; Smith, 1987). Plants carrying the gene S^F in a homozygous or heterozygous condition are highly, but not completely, protected against cross-pollination even without any isolation

measure. The trait is useful for the development of inbred lines, and it is employed in breeding programs in combination with NMS.

5 Current Goals of Breeding

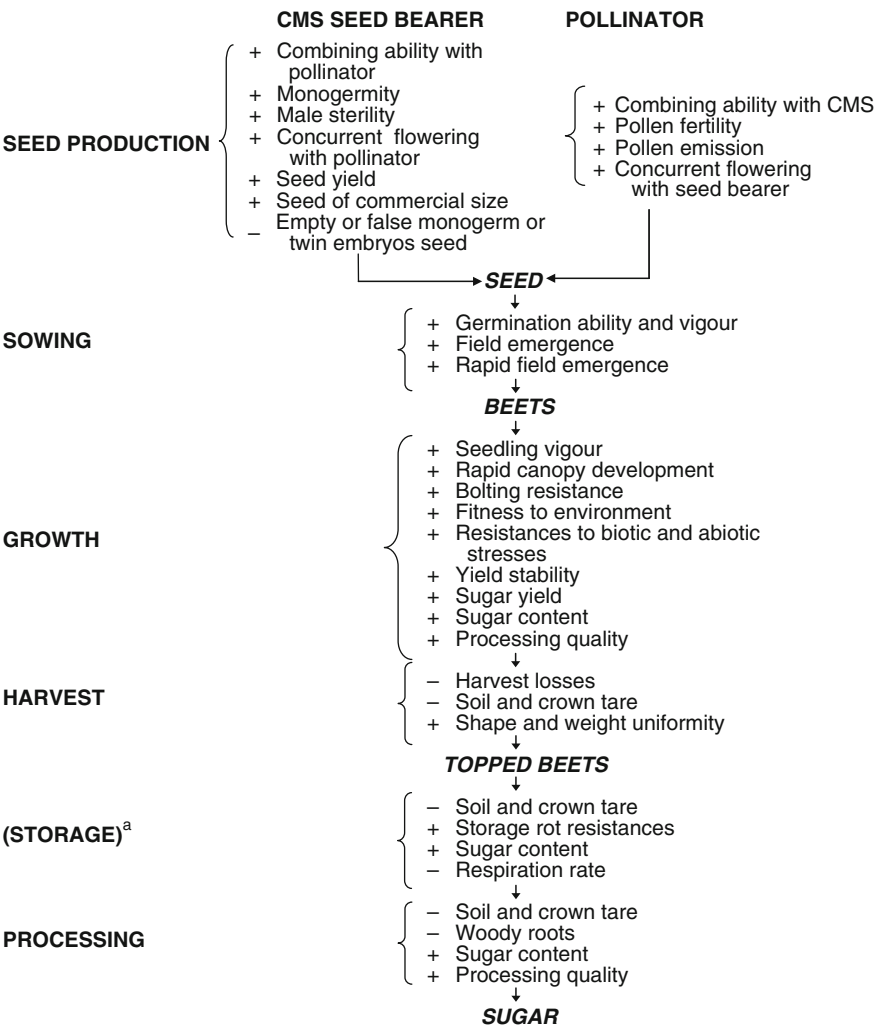
The main objective of plant breeding is the development of varieties with the maximum commercial yield at the lowest economic and environmental cost. The yield potential for sugar beets depends also on their suitability for processing, which includes several traits that enhance sugar extraction by the factory (Campbell, 2002; 2005). Varieties must also possess good yield stability across localities and years, which depend on a broad genetic base and on resistances against multiple biotic and abiotic stresses. Apart from these general objectives, several secondary breeding aims are taken into account according to local needs (Barocka, 1985). More than 40 qualitative traits were recognized as follows: annuality, monogermy, Mendelian male sterility, self-fertility, some forms of resistance to rhizomania, etc. (Smith, 1987; van Geyt et al., 1990). The improvement of composite traits, such as yield, processing quality, germination ability, bolting, and several disease resistances, is more difficult due to their quantitative inheritance and genotype × environment interactions.

In Fig. 6.4 an outlook of the selection targets in the different phases of sugar beet development and factory processing is presented. Results are still unsatisfactory for several resistances, not only for incomplete reduction of damage but also for a yield penalty that lowers sugar yield and processing quality. A complete review of the resistances against biotic and abiotic stresses in sugar beet was made by Biancardi et al. (2005).

5.1 Yield and Quality Traits

Gross sugar yield is the most important trait for growers and it depends on the weight of the roots produced per hectare and on the sugar content, i.e., the percentage w/w of sucrose present in the roots. In addition to the gross sugar yield, the extractable sugar must be considered, indicating how much white sugar can be extracted in the factory. This is directly related to processing quality (see below). With increasing quality, the white sugar yield approaches the gross sugar yield. The inheritance of the character "sugar yield" is quantitative and strongly affected by the environment (Powers et al., 1963). A non-additive variance is prevalent in controlling the trait "root production" (Campbell, 2002), while for the "sugar content" the variance is additive without expression of heterosis or dominance (Smith et al., 1973). There is a high correlation between sugar yield and root yield. However, if the root weight is increased by selection, the sugar content tends to be lower and vice versa.

Processing quality includes a number of chemical and physical traits of the harvested beets affecting the quantity of extractable sugar (Oltmann et al., 1984). Many



[a]Only in cold environments

Fig. 6.4 Breeding targets (– less; + more) of some sugar beet traits in different steps of development and processing

of such characteristics are under genetic control, but the effect of cultural practices, harvest, storage methods, environment, etc., normally exerts a greater influence than the genetic control (Harvey and Dutton, 1993). Among the soluble impurities (non-sugars), sodium, potassium, alpha-amino nitrogen, reducing sugars, etc., have received most attention in breeding programs due to their negative effects on sugar extraction (Last and Draycott, 1977; Smith et al., 1977). The concentration of these non-sugars can be easily reduced with mass selection, suggesting an additive

genetic variance (Powers et al., 1963; Smith et al., 1973; Coe, 1987; Smith and Martin, 1989). Breeding for further improvements is complicated by interactions among non-sugars, sucrose concentration, and root weight (Campbell, 2005).

Some anatomical characteristics of the roots are associated with processing quality. Selection of smooth root hybrids (with reduced or without the two vertical grooves) lowers the amount of adhering soil carried to the factory (Fig. 6.5). This is desirable as the soil remaining on the roots after washing causes damage, especially during the slicing and diffusion phases (Theurer, 1993). Smooth root varieties with improved root shape and reduced crown dimension were developed through repeated cycles of mass selection (Mesken and Dieleman, 1988; Saunders et al., 1999). Similar results in improving processing quality are also possible with an appropriate fertilizer management.

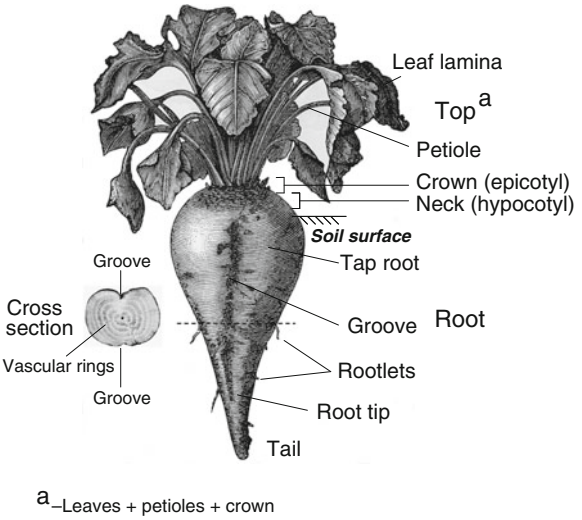


Fig. 6.5 Sugar beet drawing with the common names of the main parts

5.2 Resistance to Diseases

5.2.1 Curly Top

The beet curly top virus (BCTV) is transmitted by the beet leafhopper *Circulifer tenellus* Baker that attacks sugar beet throughout the arid areas in Western USA, Southwestern Canada, Mexico, Turkey, Iran, etc. (Duffus and Ruppel, 1993). The BCTV is a mixture of strains, which vary their virulence according to the host conditions, thus changing continuously the reactions required by the resistant varieties (McFarlane, 1971; Stenger and McMahon, 1997; Strausbaugh et al., 2008; Lam et al., 2009). Infected plants show a typical leaf curling, discoloration, and stunting, followed by the death of the young beets under severe infections. Breeding programs were initiated around 1925 by Carsner (1933). Mass selection of roots showing resistance in heavily infested fields proved effective (Coons et al., 1931), and the first resistant open-pollinated variety US1 was released (Coons, 1949). Although mass selection was successful in producing resistant open-pollinated populations,

inbreeding and progeny testing were necessary to continue to improve the varieties and to transfer the monogermy in the multigerm-resistant families (McFarlane, 1969). Much of the breeding for BCTV resistance was done through selfed genotypes endowed with the S^F gene and NMS (Owen, 1952). Improvements in creating uniform BCTV infection in selection fields have been instrumental for breeding progress (Murphy and Savitsky, 1952; Mumford, 1974).

Studies carried out by Abegg and Owen (1936) described a partially dominant genetic factor *C*, linked to the gene for crown color *R*. Murphy and Savitsky (1952) indicated a more intermediate (additive) resistance in F1 hybrids under moderate BCTV infection. In case of severe BCTV attacks on susceptible genotypes, the genetic nature of resistance appeared more composite. Savitsky and Murphy (1954) estimated that two or more genes were involved in the BCTV resistance. According to Hecker and Helmerich (1985), the multigenic traits of resistance should be present in both parents of the hybrid varieties. The genetic control of the disease was successfully integrated, and in some cases replaced, by insecticide treatments against the vector (Strausbaugh et al., 2006). Due to the need to reduce pesticides and other chemicals, further and rapid improvement of the BCTV resistance is necessary.

5.2.2 Rhizomania

This disease is caused by beet necrotic yellow vein virus (BNYVV) carried and inoculated into sugar beet roots by the soil-borne fungus *Polymyxa betae* Keskin. The symptoms are evident especially on the roots as (i) excessive proliferation of the rootlets assuming a beard-like appearance around the tap root; (ii) constrictions of the root tip leading to a wineglass shape; (iii) necrotic rings in the root tip section (Fig. 6.6). Diseased beets, if analyzed, show low sugar content, processing quality, etc. Immunoenzymatic tests (ELISA) performed on the roots can easily quantify the infection.

The virus causes losses of up to 80% in sugar yield (McGrann et al., 2009). Firstly detected in Italy around 1950, the disease is today more or less widespread in all growing areas (McGrann et al., 2009). By means of RNA analyses, three pathotypes of BNYVV were identified (A, B, and P) with different geographical distribution and pathogenic effects on the crop (Koenig et al., 1995; Lennefors, 2006a). The first source of resistance was found in cercospora leaf spot (CLS)-resistant germplasm derived from the multigerm variety "Alba P" (Biancardi et al., 2002). The superior performance of "Alba P" was observed in trials grown in 1957, i.e., before the discovery of the disease agents (Bongiovanni and Lanzoni, 1964). The resistance was classified as quantitative (Lewellen and Biancardi, 1990). A more resistant variety "Rizor" was released in 1985 by SES Italy (De Biaggi, 1987). The "Rizor"-type resistance was recognized as monogenic and dominant, being the hybrid variety produced with susceptible CMS seed bearer. In 1983, Erichsen observed some experimental hybrids yielding five times more than the mean of a diseased field trial (Lewellen et al., 1987). The hybrids, produced by the same CMS line owned by Holly Sugar Company, segregated in a pattern typical for a single

Fig. 6.6 Beets severely diseased by rhizomania

dominant gene, now named *Rz1* (Lewellen et al., 1987; Lewellen, 1988). Later, screening trials carried out in California confirmed that WB42, an accession of sea beet collected in Denmark, was resistant in diseased field condition (Lewellen, 1995a). Lewellen (1995a) identified other sources of resistance with unknown traits in the genotypes C28, R04, R05, C50, WB151, and WB169. Scholten (1997) and Scholten et al. (1999) reported that WB42 resistance was conditioned by a dominant gene, closely linked to the *Rz1* gene. This gene was coded *Rz2*. More recently, Gidner et al. (2005), Grimmer et al. (2008a), and Grimmer et al. (2008b) found similar traits of resistance in the sea beet accessions WB41 and WB258 (Panella and Lewellen, 2007).

The commercially employed types of resistance, Alba, Rizor, and Holly, appear to be derived from sea beet (Biancardi et al., 2002). The monogenic resistances in Rizor and Holly have been mapped to the same chromosomal region (Scholten et al., 1999; Biancardi et al., 2002). Genotypes carrying the monogenic sources of resistance frequently exhibit different levels of expression, probably due to the presence of minor genes interacting with the major allele in heterozygous individuals (Scholten et al., 1996; De Biaggi et al., 2003).

The resistant varieties used today, when tested in severe disease conditions applied in greenhouses, display no more than 80% resistant plants. Improvement of this percentage should allow better sugar yield even in severely diseased fields. Since the resistance in commercial varieties is usually transmitted by the pollinators, this goal should be possible using varieties in which all plants carry the genes of resistance at least in heterozygous conditions. This result is becoming possible by (i) using resistant pollinators and seed bearers; (ii) analyzing with molecular markers for rhizomania-resistance genes all pollinating and/or seed-bearing beets employed in seed production; and (iii) discarding the recessive and, when possible, the heterozygous plants. In addition, further sugar yield improvements should

be possible by combining in the same variety the different sources of resistance (De Biaggi, 2005). This would be essential where the known sources of resistance appear to be overcome by suspected mutations of BNYVV or in presence of the more pathogenic strains of the virus (Liu and Lewellen, 2007; Panella and Lewellen, 2007). Additional advantages may be obtained utilizing some forms of resistance against the vector *P. betae* found in wild species of the sections *Beta*, *Corollinae,* and *Procumbentes* (Paul, 1993; Paul et al., 1994; Barr et al., 1995; McGrann et al., 2009).

5.2.3 Cercospora Leaf Spot

Cercospora leaf spot (CLS), caused by the fungus *C. beticola* Sacc., is a very damaging disease in humid temperate zones (Greece, northern Italy, northern Spain, Austria, southern France, Japan, China, Michigan, etc.). The infection develops as necrotic lesions that enlarge and cause the more or less rapid destruction of the leaves. During the juvenile stage (up until 80–90 days from emergence), sugar beet appears immune to CLS attack, suggesting an inhibitory mechanism for the establishment of the pathogen inside the leaves. Several explanations have been proposed, such as lack of synchronization between hyphae elongation and stomata opening and the narrow passage through the stomata excluding the hyphae (Canova, 1959; Solel and Minz, 1971). None of these hypotheses were confirmed (Ruppel, 1972).

Only one source of quantitative genetic resistance to CLS is employed today (Skaracis and Biancardi, 2000). A second qualitative type of resistance has been reported when plants are infected with pathogen strains present in a limited area of California (Lewellen and Whitney, 1976). The latter resistance was not commercially employed. Species of the section *Procumbentes* exhibit high levels of resistance with unknown genetic characteristics (Biancardi, unpublished data). CLS-resistant genotypes have been derived from crosses initiated around 1915 using sea beets collected along the coasts of Adriatic Sea (Munerati, 1931). After repeated backcrossing in order to reduce the negative traits of sea beet, some resistant lines were released (Coons et al., 1955; Coons, 1975). Selections continued in Italy and in the United States, giving rise to numerous commercial varieties (Coons, 1975; Lewellen, 1992).

The CLS resistance discovered by Munerati is controlled by at least four or five alleles with variable effects depending on the severity of infection (Smith and Gaskill, 1970). Based on QTL analysis, Koch (1997) agrees with these results, attributing part of the difficulties encountered in selection to recessive genes controlling the expression of the trait. Several fungicides proved quite effective in limiting the disease. When the effects of fungicides and resistance complement each other, a satisfactory control of the disease is achieved (Skaracis and Biancardi, 2000).

5.2.4 Beet Cyst Nematode

Cyst nematode (*Heterodera schachtii* Schm.) is one of the most destructive pests of sugar beet. It damages the root system and severely limits root yield and sugar

content. Typical symptoms are the weak development of the beets and the wilted leaves under high temperature and/or intense light conditions. The cysts of the nematode can be quite easily seen on the rootlets with the naked eye. Management of nematodes in sugar beet is becoming harder due to the increasing restriction on fumigations and to the wide number of host crops and weeds. Intervals of at least 4 years between beet crops reduce the nematode initial populations below economic levels.

Interspecific hybridization with embryo rescue and grafting techniques with *Beta procumbens* was employed successfully for transferring resistance to sugar beet (Savitsky, 1960, 1975; Yu, 2005). Nineteen nematode-resistant monosomic addition lines in diploid *B. vulgaris* were identified, each carrying one chromosome from *B. procumbens.* Subsequently, 18 chromosome nematode-resistant genotypes were developed, each with a translocated fragment attached to chromosome 9 that carried the gene $Hs1^{pro-1}$ (Sandal et al., 1997). Homozygous-resistant diploid sugar beet lines have been developed but continue to possess deleterious traits from *B. procumbens* and inefficient pairing in meiosis (Yu, 1983; Heijbroek et al., 1988; Lewellen, 1995b). The positional cloning of the gene $Hs1^{pro-1}$ enhanced the possibility of transferring the resistance to high-yielding varieties (Cai et al., 1997).

Resistance to cyst nematode conditioned by dominant or partially dominant genes was recently found in sea beet (Panella and Lewellen, 2007). Varieties carrying the resistance derived from *B. procumbens* and *B. vulgaris* ssp. *maritima* were released in the United States (Lewellen, 2006, 2007) and Europe. According to Niere (2009), the former source is higher yielding than the latter, which he classified less susceptible or tolerant. Under compared infested and non-infested field conditions, Lewellen and Pakish (2005) showed that the resistance from *B. vulgaris* ssp. *maritima* greatly reduced sugar yield losses and had reduced nematode populations (Lewellen and Pakish, 2005). In both cases, crop rotations in order to reduce the nematode population density and resistance breaking biotypes are advisable.

Root knot nematode (*Meloidogyne* spp.) is not as widely distributed in sugar beet production as cyst nematode, but where it occurs can be very serious. Resistance was identified in *B. vulgaris* ssp. *maritima* and transferred to sugar beet (Yu, 1995; Yu et al., 1999; Yu and Lewellen, 2004).

5.3 Resistance to Abiotic Stresses

Several breeders with different approaches have examined resistance (tolerance) to drought, cold, heat, etc. Appreciable levels of genetic variability were observed despite the masking effects of environmental interactions (Wood et al., 1950; Wood, 1952; Srivastava, 1996; Ober and Luterbacher, 2002; Stevanato, 2005). Traits conferring such resistances were identified also in wild beets (Luterbacher et al., 1998). The potential breeding value for improving stress resistance is still unknown due to the difficulties in transferring and introgressing useful traits from the wild species to high-yielding germplasm. Pidgeon et al. (2006) found positive interactions among the yield of varieties and water availability. Drought-tolerant varieties were

characterized by their specific leaf weight and their succulence index (Ober et al., 2005), both conditioned by unknown genetic factors. For cold resistance, some degree of variance was detected in sugar beet varieties (Dix et al., 1994). According to Wood (1952), the resistances to cold and to cercospora leaf spot appeared correlated. Until now, no real improvement in cold resistance has been reported in literature for sugar beet. In the southern cultivation areas, temperature and light intensity are frequently excessive for the crop. Selection to reduce heat stress was tested by analyzing leaf chlorophyll fluorescence (Clarke et al., 1995; Srivastava, 1996). In this case as well, there was no real progress obtained.

6 Breeding Methods and Techniques

Increases realized in sugar beet production through breeding have been impressive and firstly occurred at a rapid rate (McFarlane, 1971). Mass selection was applied initially, followed by several schemes based on progeny evaluation and combining ability assessment (Smith, 1987). Further advances over the last 40 years were possible using recurrent selection methods and through various biotechnology approaches.

6.1 Mass Selection

Successful application of mass selection in sugar beet requires an adequate level of heritability for improvement (Hecker, 1967). In other words, mass selection is quite efficient for qualitative characters and gives satisfactory progresses when dealing with traits controlled by genes having significant additive effects, as in the case of sugar content (Smith et al., 1973). Root yield, being controlled by genes with non-additive action, shows poor response to mass selection, although the method is quite effective if used with non-selected materials (Bosemark, 1993).

In a typical mass selection scheme, the fields are established earlier than those of the commercial crop. The beets to be selected, also called mother beets, must grow exactly in the same condition (soil, spacing, nutrients, water, treatments, etc.). Mother beets are biennial as the cultivated ones and require overwintering to enter the reproduction phase. Normally they are selected in the first year. Stecklings, i.e., beets drilled normally in August and transplanted in the late winter, are used only for seed production. At harvest, mother beets with undesired phenotypic traits are discarded. In this stage, approximately 10% of the beets closer to the desirable ideotype are selected, i.e., those with a regular shape and without defects. After individual sampling and analysis, the selected beets are treated with fungicides and kept under appropriate temperature and light conditions to induce vernalization. The following spring, transplanted roots are allowed to intercross by open pollination in isolated fields, where the seed of the improved population is harvested for a second selection cycle.

6.2 Family Selection and Line Breeding

The evaluation of genotypes based on the characteristics of their offspring provides a more efficient means for improvement than simple mass selection. Since the middle of the 1900s, family (or progeny) selection, together with its various versions, came into common use. This method allowed the accumulation of favorable genes with additive and dominant effects (Helmerick et al., 1965; Smith et al., 1973) and was successfully used for the development of improved multigerm populations. When quantitative traits are involved, the response in advanced genotypes is quite small. Efficiency of progeny testing requires the populations under improvement to possess sufficient genetic variability for the traits to be improved. Two main methods are still employed: half-sib and full-sib progeny selection (Bosemark, 1993).

6.2.1 Half-Sib Selection

Plants selected as for mass selection (year 1) are vernalized and intercrossed by open pollination (Fig. 6.7) and the seed is collected separately (year 2). The seed of each plant, a half-sib (HS) family, is a mixture of F1 hybrids produced by the seed bearer and by a random sample of pollen released by the plants present in the crossing plot. Due to the possible presence of a variable degree of self-fertility, part of the seed of each HS family could be derived by self-pollination. The seed of the HS families is drilled in field trials to assess the yield performances (year 3). According to the results, the best HS families are selected in the nursery established in the meantime. Usually, the seed quantities of the single HS families are small and consequently the field tests are limited to few replications. The best HS families can be used to repeat years 2 and 3 (HS family selection) or individual HS families can be multiplied under pollen isolation (year 4). Higher seed quantities and reduced heterozygosity in these S1 multiplications allow a more reliable evaluation of the HS families (year 5), but will be accompanied by some inbreeding depression for yield. The stecklings of the superior S1's are joined for seed production (year 6). Field evaluation of HS families provides an indication of their general combining ability (GCA), whereas trials of their respective S1's allow the elimination of other inferior lines. In this way, a quite efficient selection is possible, but the S1 evaluation lengthens the cycle time for recurrent selection. The seed obtained at the end of the selection process can be used directly (or after appropriate test cross evaluations) as pollinators for commercial varieties. Several modifications of the method are possible.

6.2.2 Full-Sib Selection

This method allows a more effective selection because both parents of the full-sib (FS) families are fully determined (Hecker and Helmerich, 1985; Smith, 1987). As with the HS scheme, the FS selection method is mainly used for improving pollinators.

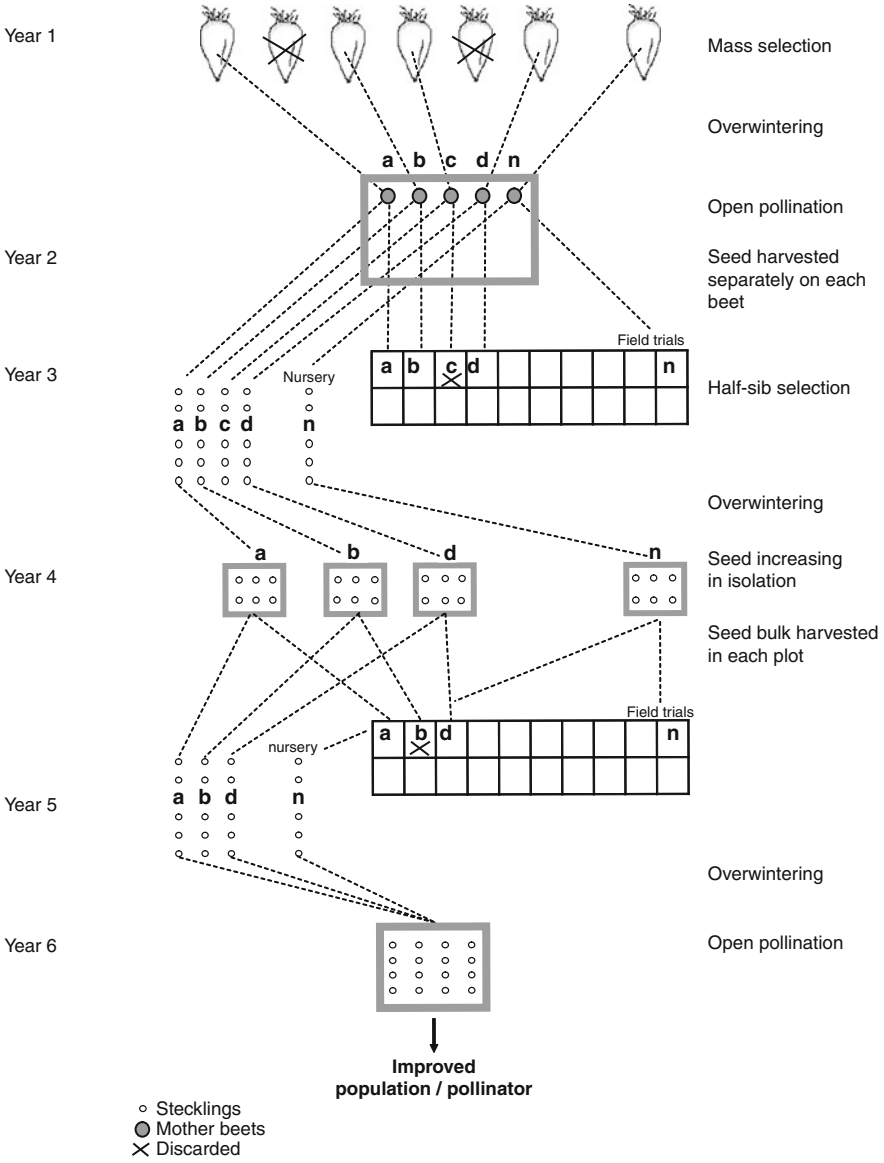


Fig. 6.7 Half-sib selection method

Through normally mass selected mother beets, seed is produced in isolated pair crosses. The new FS families are sown in the nursery and in field trials. The following year, only the better families are intercrossed to obtain an improved population with a superior range of favorable genetic combinations. As with the HS families, the seed multiplication in isolated plots (S1) of the FS families would allow

a more accurate assessment of their yield potential. However, the performance of FS families will be affected by inbreeding depression.

6.3 Recurrent Selection for Combining Ability

Recurrent selection (RS) for combining ability refers to a group of methods suited to improvements through an increased frequency of superior alleles and allelic combinations. The method allows the selection of lines with superior combining ability for use as male or female parents of hybrid varieties. The RS method presents the following common features: (i) plants of a heterozygous family are either selfed (S1) or selfed and crossed to a tester; (ii) after field trials of the S1s or test crosses, the inferior progenies are eliminated; (iii) all possible crosses between the remaining S1 progenies are performed; and (iv) the population resulting from these crosses is used to begin a new selection cycle.

Four main models of RS methods are suitable for sugar beet (Bosemark, 2006): (i) Simple recurrent selection (SRS), based solely on the phenotype or on the evaluation of S1 progenies; (ii) Recurrent selection for general combining ability (RSGCA), where the selection is made according to the evaluation of test crosses with a heterozygous common tester; (iii) Recurrent selection for specific combining ability (RSSCA), where the tester line, usually an inbred line, provides information on the specific (and general) combining ability of the selected families; and (iv) Reciprocal recurrent selection (RRS), in which two populations are simultaneously improved, in the same way as in RSGCA, but one is used as tester to the other, and vice versa. A number of other variations are possible depending on the genotypes, the traits to improve, and the selection targets.

6.4 Hybrid Varieties

With the employment of CMS monogerm lines, several new combinations of varieties became possible (Table 6.2) using as pollinators the same genotypes employed for the multigerm varieties. Seed harvested on monogerm seed bearers is genetically multigerm but phenotypically monogerm, thus only the female monogerm parent was necessary for the synthesis of the first monogerm hybrids. Crossing multigerm $2x$ line or family to $2x$ monogerm CMS line, $2x$ monogerm single cross or top cross hybrids are produced, respectively. If the CMS seed bearer is an F1 between CMS and different O-type lines, the cross with a $2x$ pollinator gives a three-way hybrid. If both parents are F1, a double cross hybrid is obtained. Using $4x$ pollinators, similar combinations at $3x$ ploidy level are possible. The use of $4x$ CMS lines is difficult due to problems of pollen contamination during seed production. Notwithstanding, crossing $4x$ CMS lines with $2x$ or $4x$ pollinators, $3x$ "reverse" and $4x$ hybrids were obtained, respectively. The former varieties were released by some European seed companies, but were not widely grown commercially (Bosemark, 1977).

Commercial varieties are produced crossing inbred CMS lines with pollinators, which can be inbred lines or hybrids between inbred lines. In these cases, single crosses (A × B) and three-way crosses A × (B × C) are obtained, respectively. For improving seed yield, usually the monogerm seed bearer is not an inbred line but a hybrid between a CMS line and a different O-type line from the maintainer. Such CMS F1 produces three-way crosses (A × B) × C or double cross (A × B) × (C × D) hybrids after crossing with an inbred line or a hybrid between inbred lines. Hybrids made with pollinators reproduced by free intercrossing (families) are designated top crosses.

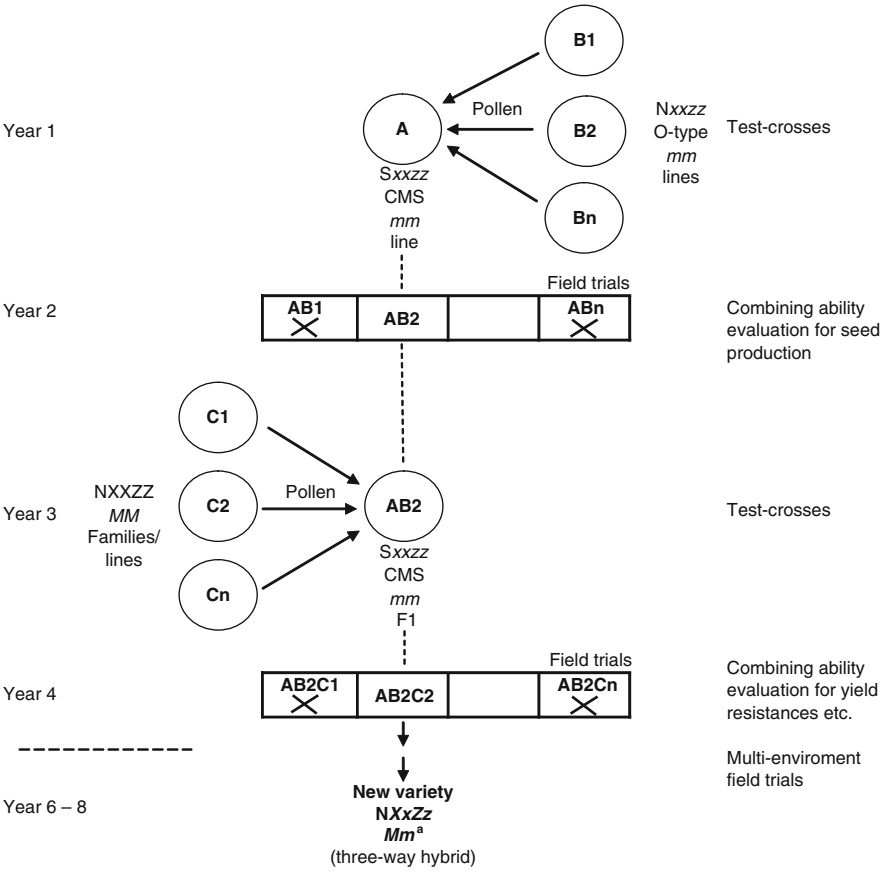
For some decades, the 3*x* hybrids obtained with 4*x* multigerm families and 2*x* CMS F1 seed bearers displayed a superior sugar yield to the 2*x* equivalents, and, at least in Europe, had large commercial success. In the last 25 years, the development of 2*x* pollinators with a broad genetic base (family) enabled the synthesis of 2*x* hybrids with improved performance. Therefore, the use of 2*x* hybrid varieties is becoming prevalent in Europe, as elsewhere, due to a simpler and less expensive breeding process, easier introgression of the resistance traits, better germination quality of the seed, and higher processing quality. Today, at least in more advanced countries, most varieties can be classified as 2*x* three-way hybrids or as 2*x* single cross hybrids. The latter combination is less frequent owing to the lower seed production of CMS lines.

Methods for the synthesis of hybrid varieties are becoming quite similar among the few seed companies currently active. In Fig. 6.8 is represented the method for the synthesis of three-way hybrids employing a monogerm CMS F1 crossed with a multigerm 2*x* pollinator. As previously mentioned, the CMS inbred line is usually crossed with a different O-type. The selection of the best combination CMS × O-type is made testing their general combining ability (GCA). The traits to consider in the F1 progeny are also seed production, a high degree of male sterility, monogermy, the traits of the seed stalk, etc. The selected CMS F1 is crossed with different pollinators each in an isolated field. The seed of test crosses is harvested from the CMS and is accurately tested for the germination traits. The year later, test crosses are drilled in multi-year field trials organized in localities where the future variety should be cultivated. The crosses with superior yield and quality performances are mixed in different ways and go on with testing for at least 3 years. According to the results, the seed of the new variety is reproduced in large amounts for registration procedures and commercialization.

7 Integration of New Biotechnologies in Breeding Programs

7.1 Genetic Maps

Many sugar beet genetic maps have been constructed with molecular markers using (i) anonymous genomic restriction fragment length polymorphisms (RFLP); (ii) randomly amplified polymorphic DNA (RAPD); (iii) amplified fragment length



[a] Monogerm because harvested on monogerm plants.
X Discarded

Fig. 6.8 Synthesis of three-way hybrid variety including tests of combining ability for O-types and pollinators

polymorphisms (AFLP); (iv) simple sequence repeats (SSR); (v) single nucleotide polymorphisms (SNP), as well as morphological and isozyme markers (Barzen et al., 1992; Pillen et al., 1992, 1993; Boudry et al., 1994; Barzen et al., 1995; Uphoff and Wricke, 1995; Halldén et al., 1996; Schondelmaier et al., 1996; Nilsson et al., 1997; Schumacher et al., 1997; Hansen et al., 1999; Weber et al., 1999; Rae et al., 2000; Schneider et al., 2001; Möhring et al., 2004; Grimmer et al., 2007a; Schneider et al., 2007). The specific numbering of individual chromosomes, defined in genetic linkage maps, has been standardized. However, most maps have not been updated to reflect a common nomenclature. A series of markers are now publically available that allow standardization of chromosome nomenclature in most, if not all, mapping populations (McGrath et al., 2007 and unpublished). Work by Schondelmaier and

Jung (1997) is now considered the reference since their work has integrated previous cytogenetic information. Schneider et al. (2001) sequenced 37 genes developed from ESTs in two inbred sugar beet lines, and found one SNP per 283 bp within coding regions, and one SNP per 130 bp if introns and 5′ and 3′ flanking sequences were also considered. In 400 specific regions defined by ESTs, Schmidt et al. (2003) showed 75% of sequences derived from 16 divergent *B. vulgaris* germplasm sources are sufficient to detect SNPs, with an average of 4.6 SNPs per 200–600 bp.

Most maps show strong clustering of markers on each linkage group, suggesting restricted genetic recombination, but this observation may be an artifact of the type of marker used (Nilsson et al., 1997). However, this trend is less pronounced using markers derived from expressed genes. Segregation distortion is common. Interestingly, the extreme segregation distortion for linkage group 5 in the sugar × red table beet maps of McGrath et al. (2007) and Laurent et al. (2007) was opposite in their transmission despite both using sugar beet as the maternal parent, with sugar beet alleles favored in the former and table beet alleles in the latter. There appears to be little or no regularity in the organization of duplicated chromosome regions in beets (Halldén et al., 1998), indicating the true diploid nature of the beet genome.

Molecular markers suggest a large amount of genetic diversity is present in wild *B. vulgaris* ssp. *maritima* that is not captured in the cultivated crops. Molecular markers have been used extensively to characterize sugar beet and related *Beta* species (Jung and Herrmann, 1991; Mita et al., 1991; Jung et al., 1993; Senda et al., 1995; Kraft et al., 1997; Shen et al., 1998; McGrath et al., 1999; Wang and Goldman, 1999; Kraft et al., 2000; Cureton et al., 2002; Richards et al., 2004; Poulsen et al., 2007; Fénart et al., 2008). Genetic diversity in cultivated beets is low compared with other beet types (Jung et al., 1993), and cultivated beets may contain only a quarter to a third of the genetic diversity present in sea beets (Fénart et al., 2008; Saccomani et al., 2009).

Markers have been used to discover the location of genes involved in the expression of quantitative traits. Candidate genes involved in the accumulation of sucrose in sugar beets were mapped to the nine linkage groups of beet, and QTL analyses for a number of agronomic traits (e.g., sugar yield, beet yield, sucrose content, and impurity levels) uncovered many potentially useful associations (Schneider et al., 1999; 2002). Loci involved in restoration of male fertility in a sterile cytoplasm, *X* and *Z*, have been located on chromosomes 3 and 4, respectively (Schondelmaier and Jung, 1997), with locus *X* located terminally on chromosome 3 (Pillen et al., 1993; Uphoff and Wricke, 1995; Hagihara et al., 2005a). A third putative locus was found ca. 15 cM from Z on chromosome 4 by QTL analyses (Hjerdin-Panagopoulos et al., 2002). Disease resistance gene analogues have been mapped in beets (Hunger et al., 2003), and these have allowed co-segregation analyses with disease resistance QTLs (Lein et al., 2007, 2008). Interestingly, a complete class of disease resistance genes, the TIR-type, is completely lacking in *B. vulgaris* (Tian et al., 2004). QTL approaches have identified chromosome regions associated with resistance to powdery mildew (Grimmer et al., 2007b), rhizoctonia crown and root rot (Lein et al., 2008), rhizomania (Gidner et al., 2005; Lein et al., 2007), *Aphanomyces* (Taguchi et al., 2009), and cercospora leaf spot (Nilsson et al., 1999; Schäfer-Pregl et al.,

1999; Setiawan et al., 2000). Generally, the genetic component of these measured traits can be portioned into 2–10 chromosome regions, and many of these could be considered oligogenic in their inheritance patterns. Association mapping approaches appear to have good potential for uncovering loci involved in agronomic and disease traits (Stich et al., 2008a, b). However, molecular marker density and phenotypic precision in open-pollinated populations and hybrids are still sub-optimal for fine mapping.

7.2 Sugar Beet Genome

DNA content (C-value) of *B. vulgaris* has been reported as 714–758 million base pairs per haploid genome, with variation reported among sub-species (Bennett and Smith, 1976; Arumuganathan and Earle, 1991). The nine chromosomes of sugar beet are morphologically similar at mitotic metaphase, and centromeres are either metacentric or sub-metacentric. A terminal constriction is on chromosome 1 and carries the major cluster of 18S–5.8S–25S ribosomal RNA genes. Highly repetitive DNA sequences comprise >60% of the beet genome (Flavell et al., 1974) and consist of numerous families of short (140–160 nt) repeating units present at high copy numbers (10^5–10^6 copies/genome) (Schmidt and Heslop-Harrison, 1996), and various classes of transposable elements (Schmidt and Heslop-Harrison, 1998; Staginnus et al., 2001; Jacobs et al., 2004; Dechyeva and Schmidt, 2006; Kuykendall et al., 2008; Menzel et al., 2008; Kuykendall et al., 2009). Organization of centromeric regions has been of interest to understand the molecular processes of chromosome segregation, to understand the process of non-disjunction, and to create plant artificial chromosomes (Gindullis et al., 2001a; Menzel et al., 2008; Jacobs et al., 2009). A generalized picture of beet chromosome structure and organization indicates that *Beta* chromosomes are substantially similar to most other dicot chromosomes, at a gross level.

In most cases, agronomic traits in sugar beet can be assumed to be controlled by genes whose product is a catalytic or structural RNA or protein. In sequenced crop plants, the number of genes is roughly assumed to be between 25,000 and 75,000, although much remains to be discovered about plant genomes. *B. vulgaris* would thus be expected to fall within this range for total gene number (Herwig et al., 2002), although significant differences in gene regulation, gene copy number, and presence or absence of specific gene classes (Tian et al., 2004) could be expected from differences in beet's form and function relative to other species in other plant families. Most *B. vulgaris* ESTs (Expressed Sequence Tags) are from sugar beet. These represent a reasonable cross section of important tissue types (root, leaf, seed, flower), including, for instance, genes induced upon nematode infection (Samuelian et al., 2004). The majority of ESTs were generated after oligo-fingerprinting of cDNA libraries (Bellin et al., 2002; Herwig et al., 2002), and there is good breadth of coverage (>18,000 contigs) but little depth for assessing the level of gene expression changes. In addition, 31,138 genome survey sequences have been deposited,

primarily derived from paired-end BAC and fosmid clones (McGrath et al., 2004; Lange et al., 2008). A number of large-insert libraries (e.g., Bacterial Artificial Chromosome; BAC) and other DNA libraries of beet have been made for various purposes, including cloning flowering genes and the bolting gene, nematode resistance genes, apomixis genes, CMS restorer genes, and centromeres (Jung et al., 1990; Kleine et al., 1995; Gindullis et al., 2001b; Hohmann et al., 2003; Hagihara et al., 2005b; Reeves et al., 2007; Jacobs et al., 2009). An oligo-fingerprinting approach to physical map construction is underway, and a draft *B. vulgaris* genome sequence should be available by 2011. It is anticipated that a genome sequence of beets will suggest means to achieve alternative uses of sugar beet beyond sucrose, molasses, and fodder.

7.3 Applications in Breeding

Using new technologies such as parallel nucleotide sequencing and gene expression profiling, breeders now have direct access to testing specific gene functions, such as those genes differentially expressed in root tissues (Bellin et al., 2002), and not just a correlation of phenotype with genotype. Basically, the internal workings of the beet plant can be made transparent, and thus allow more efficient and rational breeding targets, with results precisely measured and predictable. However, few target agronomic traits in beets have been characterized, and the level of understanding is still rudimentary. Still, some promise has realized. One of the first successful applications of such an approach in beets was to examine seedling vigor and resulted in identification of at least two biochemical pathways leading to enhancement of seedling vigor where little or no heritability was previously surmised (Sadeghian and Khodaii, 1998; De los Reyes and McGrath, 2003; De los Reyes et al., 2003). Differential gene expression analyses of mRNA profiles revealed a number of transcripts differentially regulated between extremes of high and low seedling vigor germplasm, and some were specifically expressed in the high vigor germplasm but not the low, identifying genetic targets for vigor enhancement. It should be noted that development of suitable test environments, such as the in vitro germination assays, could find use as surrogate selection criteria providing a strong association with agronomic performance.

In many cases, a tentative assessment of the biochemical pathways and overall metabolic status of a trait in a particular germplasm in a particular environment can be readily assessed, and this information can provide context and clarity as to the complexity of the phenotype. While specific genes and alleles and their contribution to phenotype are desired for breeding, gene cataloging and discovery are the current state of the art. Genes and proteins expressed during germination, early seedling development, mature beets, post-harvest processes, and disease and pest interactions have been surveyed (Samuelian et al., 2004; Bellin et al., 2007; Larson et al., 2007; Leubner-Metzger, 2007; Hermann et al., 2007; Puthoff and Smigocki, 2007; McGrath et al., 2008; Pestsova et al., 2008; Rotthues et al., 2008; Schmidlin

et al., 2008; Smigocki et al., 2008; Trebbi and McGrath, 2009), resulting in some broad insight into the patterns and processes of genes involved in development and responses to environment. However, at these levels of analyses, few genes can be unambiguously determined, and then only by association with other gene products present in databases, and thus their specific function and role in beets remain to be ascertained.

Specific genes identified by their demonstrated roles in processes important for sugar beet breeding have been sought. Map-based cloning approaches have been attempted, but this approach has been difficult in beets (Gaafar et al., 2005). More useful have been candidate gene approaches, particularly where model systems have uncovered biochemical pathways that have direct relevance for beet improvement. Specifically, the analysis of bolting and vernalization has been facilitated by flowering in *Arabidopsis* (Turck et al., 2008), with many of the genes in this pathway shared with beets (Reeves et al., 2007; Chia et al., 2008; Mutasa-Gottgens et al., 2009; Schulze-Buxloh et al., 2009). Marker-assisted selection is being practiced for at least one trait in sugar beet, that of rhizomania resistance. Commercial markers have been developed for the *Rz*1 gene, and likely *Rz*2, however, the specific primer sequences being used are proprietary and are likely different among the various breeding companies. Markers for rhizomania resistance are available in the public sector (Scholten and Lange, 2000; Amiri et al., 2009), but new ones are desired for other specific genes or alleles conferring resistance to rhizomania or other diseases (Friesen et al., 2006; Grimmer et al., 2007b).

The lack of fundamental knowledge about the number, identity, and diversity of genes and alleles present in beets is a serious hindrance to utilizing directed biotechnologies to introduce and develop novel traits in beets. Technology has matured to the point where transformation, while not easy, is possible (e.g., Liu et al., 2008) and novel and potentially easier methods are being investigated (e.g., Lennefors et al., 2006b, 2008). Tissue-specific expression and production of specialty compounds have been demonstrated using native beet promoters and native secondary compounds (Oltmanns et al., 2006; Thimmaraju et al., 2008), and these proofs of concept will allow rapid deployment of other modifications to the beet genome, either for breeding or as products in their own right. Risks and benefits associated with growing transgenic beets were recently summarized (Gurel et al., 2008; OCED, 2008).

7.4 Micropropagation and Haploidy

Beets are amenable to tissue culture, including clonal propagation through meristem culture, regeneration from callus tissues derived from virtually all plant organs, and somatic embryogenesis (Skaracis, 2005; Gurel et al., 2008). Success is somewhat dependent on the plant genotype, but can be generally achieved by manipulating the media and culture conditions, and in some cases the source explant tissue (Mishutkina and Gaponenko, 2006; Zhang et al., 2008; Xu et al., 2009). Tissue culture is primarily used in preparation for transformation, which is now

relatively routine in the major breeding companies; however, somaclonal variation has been exploited for herbicide resistance and salt tolerance (Gurel et al., 2008). Although culture of meristems for larger scale propagation generally avoids triggering somaclonal variation and preserves the source genotype, micropropagation is not a widely used technology for sugar beet variety development.

Haploid production in sugar beet (reviewed in Skaracis, 2005) has received considerable interest because of its potential for rapid inbreeding and fixation to genetic homozygosity in a single event. Unlike many other crops, anther culture has not proved useful for sugar beets for reasons that are not entirely apparent. Ovule culture has proved more successful, and gynogenetic embryos were shown to originate only from the egg cell (Ferrant and Bouharmont, 1994). The technique is laborious, lengthy, and the relatively low yield of doubled haploid plants (ca. 10%, obtained through chemically induced chromosome doubling of haploid ovules in culture) is currently insufficient for application in breeding programs (Mackay et al., 1999), particularly considering the genetic load in heterozygous breeding lines and fixation of lethal and sub-lethal alleles in doubled haploids. For genetic studies, doubled haploids can be important, and the most famous of them to date, KWS2320, derived from a monogerm breeding line, has been used as the DNA donor of most nucleotide sequence data in beets (Herwig et al., 2002).

8 Seed Production

8.1 Methods of Seed Production

Seedling vigor is a complex combination of traits that results in rapid germination, good field emergence, and the uniformity of stands (Stibbe and Märländer, 2002). With an adequate number of beets distributed uniformly, it is possible to optimize light interception by the canopy, and to reduce both the development of weeds and losses occurring at harvest due to irregular size and varied height of beets as they protrude above the soil surface (Snyder, 1963). Quality seed ensures better levels of sugar production. The change from breeding of multigerm to genetic monogerm varieties has made germination traits far more important, because fewer propagules are planted and each planted seed must produce a beet. Overplanting and thinning can sometimes be used to regulate the density of stand, but thinning is laborious and expensive.

Some geographical areas have been identified where the seed yield is better in terms of quantity and, particularly, quality. The most noteworthy of these are the lower Po Valley (Italy), southern France, Turkey, and Oregon (USA). Two systems of seed production are employed for sugar beet. Using the direct system, the genotypes to be reproduced are sown in place where seed will be harvested. Direct sowing is used mainly in Oregon and southeast France. An advantage of this method is that roots develop undisturbed in the same place, they are deeper and broader than the alternative transplanting. Consequently, lodging is less problematic, the crop requires less irrigation, and better vegetative development occurs.

The disadvantages include major losses caused by frost and the risk of weed beet contamination. Beets are spaced at greater distances than in sugar producer's fields and are thus less protected from the frost, having to survive the winter. Temperatures less than –12°C cause severe loss, particularly in monogerm materials (Campbell, 1968). Seed is planted at 6–14 cm intervals within rows that are 60–75 cm apart. A row of pollinators is sown every three or four rows of the CMS line. However, this proportion varies according to environment and to the pollen producing capacities of the pollinator (Smith, 1987). A second sowing method is to plant a mixture of monogerm and multigerm seeds in a ratio of about 10:1. All stalks are harvested, and the new monogerm and multigerm seeds are separated by grading (Hecker and Helmerich, 1985). Planting the parents in distinct rows is preferable since it allows inspection before flowering to eliminate any fertile, anomalous, or off-type plants. Furthermore, it allows trimming the stalks in order to obtain simultaneous flowering of pollinators and seed bearers.

In the indirect system, beets are first planted in a nursery. At the appropriate time, usually after vernalization, the small roots (stecklings) are transplanted into seed production fields located elsewhere (Bornscheuer et al., 1993). The system is more laborious but allows higher levels of seed quality. It is used especially in Italy and southeast France. As in the former system, there is the risk of nursery contamination caused by seed left in the soil by previous beet crops. In order to avoid such situations, it is necessary to know the past rotations of the field, and to leave at least 10 years after the last beet crop (Bornscheuer et al., 1993). Before sowing the nursery, it is necessary to know the germination ability of the genotypes, since the stand affects the dimension of the stecklings. A regular stand reduces plants wasted by a smaller or larger shape than optimal. The ideal stand is between 1,000,000 and 1,200,000 plants per hectare. The distance between the monogerm seeds in the row generally ranges between 2 and 3 cm. For multigerm seed, the distance between depends on the mean number of embryos per seed cluster. The rows are drilled from 20 to 25 cm apart depending on zone, soil, harvesting system, and climate. The nursery is normally planted in August.

The stand of stecklings at transplanting time also depends on sensitivity to cold. It is rare to find damage to multigerm pollinators, but the CMS's and especially the O-types are more sensitive. In order to avoid frost damage, special plastic covers are used to ensure effective thermal insulation. Nursery fertilization roughly follows that recommended for the sugar crop, with attention to the amount of nitrogen, which can cause excessive vegetative development. Great care is taken against diseases, such as cercospora leaf spot, *Phoma*, *Alternaria*, powdery mildew, *Botrytis*, *Pseudomonas,* and *Peronospora*. Insects (flea beetles, aphids, cutworms, etc.) also require adequate chemical control. Due to the required long rotations, control of the cyst nematode is usually not an issue. For weed control, the same herbicides employed for sugar crops are used.

Stecklings are normally harvested in February or March. In colder environments, it is better to harvest before winter and to store the plants in piles with leaves oriented toward the outside of the piles. The dimensions of the roots at transplanting depend on the stand and on weather conditions, but the most important characteristic is uniformity. Generally, roots measuring 3–4 cm across survive transplanting better.

Smaller roots are more suited to mechanical operations and require lower transportation costs, but they are more susceptible to drought. Leaves are trimmed mechanically before uprooting to leave petioles measuring 4–5 cm in length, and the tap root is trimmed at its end to stimulate development of lateral roots. Finally, the stecklings are cleaned of adhered soil and submersed in a fungicide solution to control fungal disease, such as *Phoma*.

Parents of hybrid varieties are usually transplanted into distinct rows. Stecklings are transplanted every 40–50 cm in rows 70–80 cm apart, for a target population density of about 36,000 plants per hectare. Once transplanted, only the petioles must protrude completely above the soil. It is important that the soil surrounding the stecklings is carefully compressed. Weeds are controlled with hoeing between the rows and with herbicides. Attention should be paid to *Phoma*, *Alternaria*, *Uromyces*, *Ramularia*, *Cercospora*, *Erysiphe*, *Botrytis*, *Peronospora*, *Verticillium*, and *Pseudomonas*, which all reduce yield and seed quality. Black and green aphids must be controlled, before and after bolting, due to the risk of virus infection. Any type of chemical treatment is not advisable during flowering. Irrigation after transplanting is often necessary and, if so, it should be repeated during seed ripening. An improvement of yield and quality is possible with drip irrigation, which does not moisten the plants and reduces the risk of pathogens on seeds. Topping (about 10–20 cm) of the seed-bearing stalks favors the development of lateral branches and improves the uniformity of the seed size. It is also useful to synchronize flowering of pollinators and seed bearers.

The growth of the seed stalk and development of flowers continues through harvest, in July–August. Therefore, all plants have a range of flowers under development, from fully closed, forming, and fully functional flowers, together with seeds at different stages of ripening. Pollinators are eliminated at the end of June, since flowers pollinated after this date are unlikely to be ripe by the time seed is harvested from the field. The harvest of the seed bearers begins when most of the seed has turned a light tobacco color and starts to come away easily. Earlier harvests will not lead to great losses, but the seed is partially unripe and there is the risk of poor germination. The loss of seeds increases with later harvests.

Swathing machines are adapted to avoid shaking the plants and the resulting seed shatter and loss of seed. The stalks are laid out in windrows for 1–2 weeks until seed moisture is 10–15%. Rain during this period is very damaging because it promotes the development of fungal parasites on the seeds, and always results in lowered germination. Threshing machines are also equipped for reducing the seed losses. Where the climate does not allow the drying in the field, stalks are transported to the factory to be processed as soon as possible.

Regular stands in sugar beet fields depend not only on germination ability, speed of emergence, etc., but also on other qualities, such as the percentage of empty, shrunken, or false monogerm (twin) seeds. Empty seeds are normal shaped, but they do not contain an embryo (TeKrony and Hardin, 1969; Shavrukov et al., 2000). A quite large percentage of empty seeds were observed, especially in 3*x* monogerm hybrids (Jassem, 1976). Due to their weight difference compared with normal seeds, empty seeds are partially eliminated by gravity tables. Monogerm seeds containing

shrunken embryos are impossible to discard by seed processing. The only method for reducing their percentage is careful selection of the parents, as can be judged by X-ray analysis of the hybrid seed. Another negative trait is the presence of multiple embryos in the same apparently monogerm seed (false monogermy). In this case, two, or rarely, more embryos develop. The "twin embryos" character is heritable and is quite well distributed among 4*x* genotypes and in 3*x* hybrids (Fischer, 1956). Their percentage can be reduced by separation on a gravity table, simultaneously with empty seeds.

Improvement in seed characteristics and emergence of commercial varieties is a slow but continuous process (Longden, 1990). Selection plays a significant role, but much of this progress has been due to seed crop growth and seed processing techniques and also in protecting germinating seedlings with chemicals delivered via pellet seed. Further improvement of germination traits and in speed of emergence was obtained using seed priming, which is a process of pre-germination (Mukasa et al., 2003). The use of primed seed in Western Europe and in the United States is increasing rapidly and is approaching 100% in areas such as France.

8.2 Pollen Isolation

Sugar beet is normally allogamous and self-sterile. Over medium and long distances, wind pollination is prevalent (Artschwager, 1927; Stewart and Tingey, 1927). Pollen granules are spherical with a diameter varying around 16–20 μm (Artschwager and Starrett, 1933). On 4*x* plants, the diameter is 5–10 μm greater (Knapp, 1958). The traits of sugar beet pollen are suited to be carried easily by the wind and for covering long distances.

Except for some self-fertile genotypes, control of pollination is necessary during breeding and the reproduction of basic and commercial seed. Isolation systems include (i) paper or cloth bags for one or more branches of the seed stalk; (ii) cloth or plastic coverings for one or two plants; (iii) glass and metal structures for up to about ten plants; and (iv) space isolation for more numerous groups and for commercial seed crops (Knapp, 1958). Using bags or isolators of small dimensions, the isolation can be completely controlled, but often the yield and quality of the seed are lower due to higher temperature and humidity inside the enclosure (Raleigh, 1936). Space isolation uses distance to lower effectively the pollen concentration in the air (Archimowitsch, 1949). Stewart and Campbell (1952) state that pollen levels reduce as the squared distance from the source, even if air movement and meteorological conditions create large variations.

In commercial seed production, fields must be appropriately separated to prevent or minimize possible contamination. The "home" pollen, with which fertilization is planned, could be mixed with "foreign" (contaminating or background) pollen released by other *Beta* sources (Chamberlain, 1967). Damage caused by pollen contamination on commercial seed multiplications depends not only on the percentage of undesired crosses, but also on the origin of the pollen itself. Although rare, crosses

with wild beets, like sea beet and *B. macrocarpa*, are very damaging due to the transmission of the annual trait. More commonly, contamination is due to weed or ruderal beets, i.e., from plants originating from the seeds of bolted sugar beet growing inside or outside of cultivated fields, respectively. Since weed beets can receive pollen released up to 9.6 km apart (Marco De Biaggi, personal communication), intercrossing is almost unavoidable in some areas (Fenart et al. 2007). If cultivation of transgenic varieties is allowed, the risk of transmission of the modified traits from the cultivated to the weed beets needs to be taken into account (Bartsch et al., 2003).

As the annual trait is dominant, the pollen of wild, ruderal, and weed beets transmits this bolting habit to the progeny. In seed production areas, damage caused by the pollen emitted by bolted sugar beets is quite frequent. Therefore, bolting sugar beets should be eliminated before the flower's opening. Crosses between other types of cultivated beets (leaf, garden, fodder) are also dangerous because they are immediately recognizable in the subsequent sugar beet crop, even if the contamination is very slight.

Crosses can also occur between fields where the seed of different varieties is produced. Morphological and agronomic differences between the commercial pollinators are generally so small that the contamination is difficult to detect, unless there are differences in chromosome number between the pollinators. In such case, if the field is to produce 3*x* hybrids, the presence of foreign pollen released by 2*x* beets causes an increased percentage of 2*x* hybrids. Risks of contamination by pollinators are much lower in fields for producing 2*x* hybrids, as this foreign pollen is less competitive (Scott and Longden, 1970). The minimum distance between seed crops required by law generally leads to low and acceptable levels of contamination if the annual and bolting beets are eliminated in a timely fashion around the fields.

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