6 Beet

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6.1 Introduction

6.1.1 Brief History of the Crop

The earliest use of beets, likely prehistorical, was leaves harvested from wild plants and used for food (Coons 1936; Ford-Lloyd et al. 1975; de Bock 1986; Lange et al. 1999). Selection likely first transformed the annual habit into the biennial habit characteristic of all current crop types, conserving and propagating germplasm for their leaf quality, the only part utilized at that time (Biancardi 1999). Sweet, swollen roots were probably selected from leafy beets, likely bearing resemblance to the chard of today, cultivated in Assyrian, Greek and Roman gardens (Ford-Lloyd et al. 1975). Traits such as the swollen red root were desired since the middle ages in Europe (Pink 1993), originally selected for its use as a leaf vegetable in the Mediterranean region and then later for use as a fresh or stored root vegetable (Campbell 1976) and as one of the first sources of dietary sweeteners available during the winter months. Later in the Middle Ages, the use of beet root was expanded to include animal feed, and the fodder beet became an important component of European agriculture by the nineteenth century. Beets grown exclusively for sucrose are of relatively recent origin (von Lippmann 1925), economic production was begun in Germany and some years later by edict in Napoleonic France under British blockade of sucrose from tropically grown sugar cane (Winner 1993). Beets with higher levels of sucrose were selected from a white fodder beet variety. The White Silesian variety is still considered to be the primary source of sugar beet germplasm grown today (Fischer 1989). In the following century, sugar beet cultivation expanded to other temperate climates of the world and more recently into warmer climates such as in Northern Africa (Winner 1993). Sea beet (*Beta vulgaris* ssp. *maritima*), the presumed ancestor of the cultivated types, is now common along the Mediterranean coastline and the central and northern Atlantic coasts of Europe and to a lesser extent inland (Ford-Lloyd et al. 1975). Dissemination of wild seed may often be by ocean currents since the fruit is buoyant and most extant wild populations are found within 10 meters of mean sea level (Doney et al. 1990).

Cultivated varieties include leaf beet (e.g., chard), garden beet (e.g., table or red), fodder beet and sugar beet. Molecular marker evidence suggests greater diversity is present in wild *Beta vulgaris* ssp. *maritima* relative to cultivated germplasm. All types are freely crossable and give fertile offspring, although distorted segregation in advanced generations may be observed presumably due to high genetic load in this outcrossing species. It is clear that molecular markers are useful for characterizing sugar beet germplasm (Mita et al. 1991). Ninety-five percent of molecular markers tested discriminated between *Beta* species in sections *Beta* and *Patellares* and 43% of the genomic clones detected variation between tested *Beta vulgaris* cultivars. A relatively large number of *Beta* accessions were examined at ribosomal RNA encoding genes (Santoni and Bervillé 1992). Most *Beta vulgaris* germplasm, including sugar beets, was monomorphic for a particular type. Interestingly, variants were found in Swiss chard. *Beta vulgaris* ssp. *maritima* contained the greatest diversity among all accessions analyzed. Another study scored 111 polymorphic fragments across 41 diverse accessions of cultivated and wild beet (Jung et al. 1993). Genetic diversity in cultivated sugar beet germplasm was found to be low compared with other beet types and wild species. Diversity within crop types has been investigated most intensively within sugar beet (Jung et al. 1993; Hjerdin et al. 1994; Kraft et al. 1997; McGrath et al. 1999; Wang and Goldman 1999), currently the most important economic crop

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of the group, and while diversity is reduced in sugar beet relative to sea beets, evidence is consistent with all crop types having been selected from within the wild sea beet germplasm pool. Wild species diversity is viewed as a potential source of novel agronomic alleles (Frese et al. 2001).

6.1.2 Botanical Description

Cultivated beets are herbaceous, dicotyledonous plants in the genus *Beta*, in the *Chenopodiaceae* family. The genus is divided into four sections (*Beta*, *Corollinae*, *Nanae*, and *Patellares*) and includes, as well as all cultivated beets in section *Beta*, 11 other species with little or no commercial value but useful as sources of genetic traits (Ford-Lloyd et al. 1975; Lewellen 1992; Letschert et al. 1994). Species of sections *Patellares*, *Corollinae*, and *Nanae* have more limited geographic distribution than section *Beta*, and are found on various European islands of the Atlantic Ocean and coastal and inland locations from Greece to Iran (Ford-Lloyd et al. 1975; de Bock 1986). Each section is described as being progressively more difficult to hybridize with *Beta vulgaris* (Coons 1954; Letschert et al. 1994) and showing less affinity with *B. vulgaris* in chromosome pairing behavior (Nakamura et al. 1991) and repetitive DNA sequences (Schmidt and Heslop-Harrison 1993, 1998).

The cultivated crop, generally harvested in the first year after sowing, is the nonreproductive tissues, either petioles or leaves in the case of the chard and leafy types, or roots in the remaining crop types where end use in suggested in the common name. Leaves differentiate to form a rosette; their size can vary in relationship to genotype, plant stage, climatic conditions and the presence of leaf diseases (Klotz 2005). The first pairs of leaves are horizontally oriented to maximize light interception and subsequent leaves have a more erect position. In root types, a conical and lengthened taproot forms early during development and continues to enlarge during the growing season. Sucrose and pigments accumulate in vacuoles of parenchyma cells, located in between concentric cortical rings that are a unique and distinguishing feature of beets (Artschwager 1926; Hayward 1938; Doney et al. 1981; Elliott and Weston 1993).

Following a period of near freezing temperatures with long nights (vernalization) (Smit 1983; Elliott and Weston 1993), the rosette forms into a flower stalk with indeterminate inflorescences. Flowers are perfect and wind pollinated, and insect pollination occurs at a low frequency (Artschwager 1927). Inflorescences are green and sessile, and their number varies from two to many. The calyx is composed of five parts, which are adherent at the base of the ovary. There are five stamens inserted in a ring at the base, which secrete uncharacterized aromatic substances. The anthers are separated into two loggias, each of these made up of two pollen sacks. A pistil and a tricarpelate ovary, positioned on the structure that includes the ovule, form the gynaecium. The style is very short and terminates with a three- or four-lobed stigma that persists in the mature fruit. Beet pollen is spherical from 15 to 20 μm in diameter; each flower can produce up to 85,000 pollen grains (Knapp 1958). Self-fertilization rarely occurs, partially because the male and female organs of the same flower become active at different times but also due to a complex system of self-incompatibility (Lundqvist et al. 1973). The duration of the flowering period may be 40 or more days. After fertilization, flowers in the same cluster borne in axils gradually bond at the base to form the seed cluster (seedball), a corky and round structure of about 4–6 mm in diameter botanically classified as a glomerule or utricle. The true seed has a thin, pigmented seed coat that is easily separated from the seed, and contains a maternally-derived perisperm that serves as a carbohydrate reserve, the vestigial endosperm and the embryo consisting of two lipid-rich cotyledons and the axis. On germination, the seed imbibes water through the vascular architecture left by the peduncle, and the axis elongates and forces open the operculum (seedcap) at the sites of lowest tissue resistance (Taylor et al. 2003). If the seed has been placed at the correct depth in the soil (about 2 cm), emergence occurs in one to three weeks depending on temperature. The relatively small true seed is part of the problem in obtaining uniform emergence.

The normal two year breeding cycle can be hastened by seed or seedling vernalization, or by the use of a single dominant gene *B* that confers an annual habit (Abegg 1936; Bosemark 1993). The outcrossing behavior of beet can be circumvented by a dominant gene for self-fertility, S^f (Owen 1942). Inbreeding depression is one consequence of using S^f in a breeding program. A number of inbred lines have been developed using S^f in conjunction with the Mendelian recessive for male-sterility (*aa*), and this

has allowed alternative breeding schemes beyond traditional population improvement methods (i.e., mass selection, recurrent selection), which dominates most sugar beet and other crop-use breeding (Hecker and Helmerick 1985; Bosemark 1993). Red beet breeding has relied on S^f for many years (Goldman and Navazio 2003).

DNA content (C-value) of *Beta vulgaris* is reported to be 714 to 758 million base pairs per haploid genome ($n = x = 9$), with variation reported among subspecies (Bennett and Smith 1976; Arumuganathan and Earle 1991). The nine chromosomes of sugar beet are morphologically similar at mitotic metaphase, with the exception of centromeres either metacentric or submetacentric and the presence of a terminal constriction, or satellite, on chromosome 1 (Bosemark and Bormotov 1971; Nakamura et al. 1991). The terminal constriction on chromosome 1 carries the major cluster of 18S-5.8S-25S ribosomal RNA genes and ca. 20 copies at an unlinked locus (Schmidt et al. 1994). The 5S ribosomal RNA genes of *Beta vulgaris* have been cytologically and genetically located to an interstitial site near the centromere on chromosome IV (Schmidt et al. 1994; Schondelmaier et al. 1997). Most crops are diploid ($2n = 2x = 18$), although triploid hybrids are common in sugar beet (Bosemark 1993), and species in other sections have been described from diploid to pentaploid, all based on $x = 9$ chromosomes (Smith 1980). Monosomic and nullisomic plants have not been recovered, indicating the true diploid nature of the crop, and cytogenetic results are supported by linkage analyses of molecular markers where a lack of extensive chromosome duplication is documented (Schondelmaier et al. 1996; Halldén et al. 1998). However, duplicated genes may be more common. In preliminary experiments using 17 ESTs as probes against a BAC (bacterial artificial chromosome) library with six sugar beet genome equivalents, an average of 13 BAC clones per probe was identified (2.6 genes per probe per genome equivalent), with a range of 1 to 39 BAC clones identified per probe (McGrath et al. 2004).

Trisomic series have been obtained (Butterfass 1964; Romagosa et al. 1987), all but one are morphologically distinguishable. Chromosome nomenclature, defined in genetic linkage maps, has only recently been standardized, based on work by Schondelmaier and Jung (1997) integrating previous cytogenetic information based on the Butterfass trisomic series. Thus, many published maps are not concordant. It is presumed that individual chromosomes are homoeologous within the genus *Beta*, and between the crop types, but this remains to be demonstrated.

Highly repetitive DNA sequences constitute 60% or more of the beet genome (Flavell et al. 1974). Excluding ribosomal RNA repeats, the highly repetitive fraction of the genome consists of many families of short (140 to 160 nt) repeating units each with high copy number ($>10^5$ copies per genome) (Schmidt and Heslop-Harrison 1996) and transposable element-like sequences (Schmidt et al. 1995; Staginnus et al. 2001). Each chromosome in sugar beet has a characteristic pattern of repeat-sequence distribution, further supporting the true diploid nature of beet with little or no duplication of the primary chromosome set (Schondelmaier et al. 1996; Halldén et al. 1998). Highly repetitive sequence diversity is high among *Beta* genomes, especially between sections, and has proven an advantage in characterizing interspecific hybrids in *Beta* (Desel et al. 2002).

The sugar beet mitochondrial genome is 368,799 bp and has a 43.9% G+C content (Kubo et al. 2000). The beet mitochondria genome, as represented by a single male-fertile genotype, is over twice as large as the chloroplast genome (368 kb), and encodes 59 recognizable genes. Duplicated sequences, introns, unidentified open reading frames, and foreign sequences imported from the chloroplast and nucleus comprise much of the mitochondrial genome. Twenty-three mitochondrial cytotypes have been described in beets, and nonrandom associations between chloroplast and mitochondrial cytotypes may indicate common cytoplasmic ancestry in some populations of sea beets (Desplanque et al. 2000). Only two cytotypes have been economically important in the deployment of cytoplasmic male-sterility for hybrid seed production; sterile and fertile or normal (Owen 1945). These two mitochondrial genomes differ by at least 15 structural rearrangements including 35 kb of DNA inserted in five regions of the sterile cytoplasm (Kubo et al. 1999). Ivanov et al. (2004) identified specific markers associated with male-sterility in sugar beet that correspond to the transcribed genes of the mitochondrial genome. The interactions between nuclear-cytoplasmic genome are fundamental in determining the expression of cytoplasmic male-sterility used in producing commercial sugar beet hybrids (Bosemark 1993).

6.1.3 Economic Importance

Sugar beet crop supplies about a quarter of the world's consumption of sugar; sugar cane produces the remainder. While cane grows in tropical climates, sugar beet finds its best conditions in continental climates that are characterized by moderate temperatures and uniformly distributed rains. The cultivation of sugar beet is distributed among 40 countries over a total surface area of approximately 7 Mha, from which about 37 Mt of sugar are produced. The largest sugar beet cultivated areas are situated in European countries (Ukraine, Russia, Germany, France, UK, Italy, Spain, etc.). Large cultivations also exist in Asia (China, Turkey, Iran, Japan, Moldova, etc.), in the Americas (USA, Canada and Chile) and in northern Africa (Morocco, Egypt and Tunisia). Production statistics of other crop types are not widely available. Table beet and chard are grown nearly worldwide, especially important in Eastern Europe, but generally for local markets. Commercial production of red table beet for canning in the US rarely exceeds 6,000 ha per year. Fodder beet is important in Europe and Canada.

According to Alexander (1971), sugar beet taproot constituents can be divided in water (75%) and dry matter (25%). Soluble solids (20%) and insoluble solids (5%) are the main components of the dry matter. Sucrose is about 16% of the soluble solids and the remainder (4%) are so-called nonsugars or impurities, which can be eliminated or reduced due to their negative effects on sucrose crystallization. Nitrogenous compounds that are particularly noxious to sugar processing, compose 1.8% of nonsugars. Among the nitrogen-free organic compounds (1.4%) can be cited glucose and fructose, which are monosaccharides derived mainly from sucrose. The remainder is composed of soluble mineral matter (0.8%). Table beets have similar nutrient profiles, with perhaps a slightly reduced proportion of sucrose. Table beet products are good dietary sources of potassium and folic acid, low in protein, and the betalain pigments have potential as antioxidants.

6.1.4 Breeding Objectives

Selection objectives in each of the cultivated types were, and are, quite different. An impressive modification of the plant morphology is evident, not only among the cultivated types themselves, but also among extant wild beet populations. In garden, fodder, and sugar beets, the shape and the composition of the root became completely different from wildtypes, whereas in the leaf beet, only the foliar apparatus has been remarkably modified (Biancardi 1999). Common pathogens do not discriminate between crop types, so breeding for resistance is a common feature of all beet improvement programs. Often, resistances will have been identified in sugar beet and then transferred to other crop types (Goldman and Navazio 2003).

Specific breeding objectives of table beets are root shape and color, and for chard are leaf and petiole characters and color. The primary pigments in beet are the betalains, a unique class of alkaloid pigments found primarily in the Caryophyllales and some fungi (Stafford 1994). Betalain pigments are comprised of the red-violet betacyanins and the yellow betaxanthins. Both are derived from betalamic acid following the cleavage of L-DOPA between the 4- and 5-positions, and differ from one another by conjugation of a substituted aromatic nucleus in the 1,7-diazaheptamethinium chromophore (Fischer and Dreiding 1972; Clement et al. 1994). The cleavage of L-DOPA results in two intermediates, 4,5-secodopa and cyclodopa glucoside. The former intermediate is converted into betalamic acid, which in turn condenses with cyclodopa glucoside to form both betacyanin and betaxanthin. Glycosylation occurs both before and after the condensation reaction, and both pigment molecules contain glucose residues.

Alleles at two linked loci (*R* and *Y*) condition production of betalain pigment in the beet plant (Keller 1936). Color patterning in the beet plant is affected by these *R* locus alleles as well as alleles at the *Y* locus. Red roots are observed only in the presence of dominant alleles at the *R* and *Y* loci, while white roots are conditioned by recessive alleles at both loci. A *yy* condition coupled with *rr*, which is characteristic of most sugar beet cultivars, produces no betacyanin and produces betaxanthin only in the hypocotyls. Betalain pigments extracted from red beet roots provide a natural alternative to synthetic red dyes. Betalains have been successfully used in commercial food coloring operations for a number of years (von Elbe et al. 1974). Red beet dye use is increasing in a number of products, and breeding for increased dye concentrations has the potential to be substituted for other dyes while simultaneously providing antioxidants to the diet. Several

investigations suggest additional loci play a role in the quantity of betalain synthesized in the beet root (Watson and Gabelman 1984). Betalain pigment concentration responds to selection in a quantitative fashion. Pigment levels increased an average of 45% in three cycles of selection (Wolyn and Gabelman 1990), and additional gains have been possible (Goldman et al. 1996).

For fodder beet and sugar beet, the primary breeding objective is yield (Frandsen 1958; Knapp 1958; Barocka 1985). For sugar beet, the prime concern is, of course, the yield of white sugar, which at its most fundamental level is a product of a beet's sucrose percentage and its weight. Early breeding resulted in quick improvement in percent sucrose. By 1900, sucrose levels had risen from the 3–6% level reported in the earliest materials to the 12–18% level commonly seen in modern varieties. The genetics of sucrose percentage were detailed by Savitsky (1940). That data suggests two to four major genes control sucrose percent in crosses among divergent types such as sugar (15–20% sucrose), fodder and red beets (3–12% sucrose each) or chard types (12–15% sucrose). Further experiments have confirmed that sucrose percentage is a quantitatively controlled trait with high heritability (Culbertson 1942; Powers 1957; Powers et al. 1963; Zhao et al. 1997). Processing quality is an important sugar beet breeding objective, and is affected by the proportion of sucrose to total soluble solids. By-products of factory processing are: (1) molasses used for the production of ethanol, glutamate, glycine-betaine, and as a nitrogen source in bioreactors; (2) pulp for animal feed; and (3) lime ($CaCO_3$) used for improving acid soils (McGinnis 1971). Processing quality includes several characters that affect the quantity of sugar extractable from the processed roots. Many of the traits that influence quality are under genetic control, but the effect of environment, cultural practices and storage conditions frequently prevails and confound the genetic differences. Among the impurity components (called also nonsugars) sodium, potassium, and amino-nitrogen received the main attention (Campbell 2002). In many cases, their concentration in the roots can be reduced with few mass selection cycles (Powers et al. 1963), suggesting that additive genetic variance is prevailing in determining the single factors of processing quality.

The main target of sugar beet breeding is the development of varieties with the maximum sugar yield at the lowest economical and environmental costs (Knapp 1958). Therefore, the cultivated varieties must be adapted to specific agro-climatic conditions occurring in the different production environments (Barocka 1985). Sugar beet breeders are also involved in the traits related to seed multiplication of commercial varieties. From this point of view, production of seed with high germination ability is important. This trait influences the uniformity of field populations and has a significant effect on sugar yield. The plantlets need to develop quickly, so that the leaves can cover the interrows as soon as possible for the best light interception.

The improvement of sugar yield may be achieved by increasing not only the photosynthesis efficiency and the sucrose accumulation in the roots, but also the traits related to make easier the mechanical harvesting and to reduce the postharvest storage losses. It is also possible to improve the physical and chemical traits of the root tissues to enhance the efficiency of the extraction processes, such as decreasing through selection the concentration of components, including nitrogen compounds, monosaccharides, sodium, potassium, etc. (Campbell 2002).

In the southern areas of cultivation characterized by mild winters, autumn sowing to avoid summer drought is practised. In this case, the varieties must be carefully selected for bolting resistance. In fact, the winter conditions of low temperature and photoperiod favor the beginning of the reproductive phase which are the origins of the development of stalks, flowers and seed. The presence of bolted or annual beets lowers the sugar yield and the seed developed by these beets give rise to infestations of weed beets that become very difficult to control (Smit 1983).

6.1.5 Classical Breeding Achievements

Sugar beet, as the other types of cultivated beet, was initially diploid ($2n = 2x = 18$). The first tetraploid sugar beet families, having twice ($2n = 4x = 36$) the normal chromosomes, were obtained around 1940 with the employment of the mutagenic properties of colchicine (Schwanitz 1938). Plants from the two ploidy levels were crossed, producing triploid ($2n = 3x = 27$) hybrids (Bosemark 1993). Triploid hybrids, manifesting morphological characteristics intermediate to the parental ploidy levels, were commercially of interest especially in Europe, where these hybrids display a slight productive superiority, at times yielding 10% more than the diploid average. In some cases,

better disease resistance, as against Cercospora leaf spot, was observed (Skaracis and Smith 1987).

Two exceptional advances in sugar beet breeding during the twentieth century have had a tremendous impact on the economic viability of sugar beet production in the US and the world, cytoplasmic male-sterility (CMS) and monogerm seed. These developments have some, lesser impact on other crop types. Restoration of male-fertility in a sterile cytoplasm is conditioned by alleles at two unlinked loci, *X* and *Z* (Owen 1945). Both must be recessive in the seed parent for expression of male-sterility. Maintainer lines, known as O-types in sugar beet and B-lines in table beet, are also doubly recessive but fertile because of a normal cytoplasm. The process of selecting for O-type requires that each individual in the population under development be tested against a CMS-tester line and the progeny evaluated for male-sterility. Although some phenotypic differences in the restorative abilities of *X* and *Z* have been reported (e.g., male-fertility is higher when an *X* allele is dominant versus *Z*), in practice it is difficult to discriminate between their effects. In addition, the O-type must carry as many useful traits as possible, including high sucrose concentration, high general combining ability, tolerance to a wide range of biotic and abiotic stresses and good seed yield potential, as well as monogerm seed.

The second exceptional advance in sugar beet breeding has been the development of genetically monogerm seed (*m*), first found as a variant in a commercial seed production field (Savitsky 1950). Current agronomic practices require that O-types also be monogerm where each seed ball has only one seed embedded within it. In the wild condition, beet seedballs contain an average of three to four seed each. Many seeds germinate and compete with one another, and it was necessary for growers to spend >100 hours/hectare for singling the crop to a stand of about 100,000 plants per hectare. The selection of genetic monogerm seed and the use of precision seed drills permitted the required stand without hand singling.

All commercial sugar beets grown in the developed world are hybrids. Most sugar beet breeding programs have at least two components; a seed parent development program geared towards developing O-type populations and a pollinator program geared towards breeding for problems associated with unique and diverse growing regions. New characters are difficult to introgress into open-pollinated seed parents. Pollen parents are generally multigerm, open-pollinated and mass selected for disease resistance, and thus it is easier to fix resistance alleles in pollinators than in seed parent lines. Locally adapted hybrid combinations are made using pollinators selected for performance under region-specific growing conditions. Hybrids are generally heterozygous for disease resistance alleles, and this can reduce efficacy of resistance relative to breeding lines. In some areas of the world, multigerm open-pollinated, as well as hybrid, varieties are popularly used because either stand establishment is problematic or labor costs to singulate seedlings are low.

In several cultivation areas, the growers require varieties endowed with resistance to specific diseases, because the cultivation of resistant varieties reduces costs, toxicity and environmental damage associated with chemical protection. In some cases, the genetic resistance is the only means for avoiding losses, for instance resistance to the diseases rhizomania and curly top (Coons 1936; Hecker and Helmerick 1985). Several types of genetic resistance against beet diseases (e.g., rhizomania, Cercospora leaf spot, cyst nematodes) have been transferred from wild beet species to the cultivated varieties (Lewellen 1992; Biancardi et al. 2002). Severe reductions in sugar yield are frequently caused by the cyst nematodes (*Heterodera schachtii*). Resistance from *Beta procumbens*, was transferred to sugar beet by Savitsky (1975), but the yield penalty of this resistance has been difficult to overcome. Programs on hybridization with the species of section *Patellares* were initiated later in Europe (Speckmann and de Bock 1982). Various nematode-resistant monosomic additions in diploid sugar beets were established, each carrying a chromosome segment from *Beta procumbens* (Yu 1982).

Genetic resistances for other pathogens were identified and commercially exploited, e.g., against Rhizoctonia root rot, downy mildew, powdery mildew, etc. (Whitney and Duffus 1986; Biancardi et al. 2005), but each of these pathogens remains a problem today. Many efforts for developing resistances to abiotic stresses were made in different countries. An extensive list of germplasm releases by the USDA over the last 70 years underscores the importance of breeding and germplasm improvement to industry (Doney 1995). Systematic screening of the 2500+ *Beta* accessions in the National Plant Germplasm System identified additional sources of resistance within the primary gene pool (Panella 1996).

Cercospora leaf spot caused by the fungus *Cercospora beticola* is perhaps the most problematic disease of humid and temperate zones. The fungus de-

velops typical necrotic lesions on the leaves. Only one source of partial, quantitative, genetic resistance is available for breeding (Skaracis and Biancardi 2000). A second qualitative type of resistance named C2 has been reported when plants are infected with Cercospora strains from California (Lewellen and Whitney 1976). The first mentioned type of Cercospora leaf spot resistance is controlled by at least four gene pairs with variable effects depending on the severity of infection (Smith and Gaskill 1970). Chemical treatments, together with genetic resistance, provide quite effective protection.

Rhizomania is caused by the *beet necrotic yellow vein virus* (*BNYVV*) carried and transferred to sugar beet roots by the fungus *Polymyxa betae*. The virus is common in most cultivation areas and causes losses of up to 80% of the potential sugar yield. Resistant varieties, which currently provide the unique protection against the disease, are the result of three decades of breeding efforts. The first source of resistance to rhizomania was discovered in Cercospora leaf spot resistant germplasm derived from the multigerm variety Alba P (Biancardi et al. 2002). Based upon segregating F_2 populations, this resistance was classified as quantitative. A more resistant variety Rizor was released in 1985 and this resistance was recognized as monogenic and dominant as hybrids produced segregated in a pattern typical of a single dominant gene, *Rz1*. An additional monogenic resistance (*Rz2*) was identified in a sea beet population coded WB42 (Scholten and Lange 2000).

6.1.6 Classical Mapping Efforts

Inheritance of two color genes, *R* conferring a red root phenotype and *Y* conferring a yellow root phenotypes was the first demonstration of linkage (ca. 8 cM) in beets (Keller 1936), followed closely with demonstration of this group's linkage with the bolting gene, *B* (ca. 15 cM from *R*) (Abegg 1936). This now famous $Y - R - B$ linkage group was further extended (summarized in Smith 1980), and until 1980, only one other linkage group was found based on segregation of morphological markers alone. Goldman and Austin (2000) proposed a gene for blotchy color distribution (*bl*) in the root linked to the $Y - R - B$ group, however this should not be confused with an earlier gene conferring black root (*bl*) whose linkage has not yet been assigned (Smith 1980). Relatively few morphological phenotypes have been examined for Mendelian segregation and linkage beyond the 42 summarized by Smith (1980), except for the (linkage not determined) fasciated flower stalk (*ffs*) characterized in red beet by Goldman (1998). A stem fasciation character (*fas*) was also found in sugar beet to be loosely linked with monogerm seed (*m*) at ca. 27 cM (Wagner et al. 1992).

The relatively few morphological markers described in beet arises as a consequence of its outcrossing nature, where it is difficult to obtain inbred lines needed to uncover recessive alleles in populations. The ease by which pollen disseminates by air currents also hinders calculating precise linkage relationships since pollen contamination (as well as putative lethal alleles) disturb segregation ratios, although this is changing with wider deployment of the dominant S^f allele that renders controlled-cross F_1 hybrids self-fertile. Sensitivity of morphological marker phenotype expression due to environmental variability is also a concern, and isozyme characterization has been useful in developing further genetic loci in beet. Most of this work has concentrated on sugar beet, however results should hold throughout the species, and gene nomenclature should be standardized across the species without regard to crop type.

A number of isozyme marker systems have been deployed to examine linkage and genetic diversity in beets, with better results than using morphological markers due to their general independence from environmental conditions. Various authors have investigated seed storage proteins (van Geyt and Smed 1984) and as many as 13 isozyme systems (Wagner et al. 1992), with polymorphism evident in most cases, and greater diversity found among nonsugar and wild allies as compared to sugar beet where examined (Abe and Shimamoto 1990; Aicher and Saunders 1990). The locus nomenclature has not been standardized, and distorted segregation is common. Linkage was found between various isozyme markers (Abe and Tsuda 1987; van Geyt et al. 1990; Abe et al. 1992, 1993), but more importantly linkage of isozyme loci with morphological traits was characterized. The association between the color locus, *R*, and isocitrate dehydrogenase (*Icd2*) was uncovered and extended multiple times (Smed et al. 1989; Wagner et al. 1992; Abe et al. 1993; Pillen et al. 1993). Stem fasciation, monogerm seed, and four isozyme loci have been linked (Abe et al. 1992; Wagner et al. 1992), and other tentative linkage groups could be defined via cosegregation of CMS restorer loci with isozyme loci (Abe et al. 1992; Wagner et al. 1992; Pillen et al. 1993). Two groups have sug-

gested linkage between a phosphoglucose isomerase (PGI) locus and the S^f self-fertility locus segregating in self-fertile by self-sterile derived genetic populations based on highly distorted segregation ratios (Aicher and Saunders 1990; Abe et al. 1993). Trisomic analyses, based on the Butterfass (1964) series, located five isozyme loci to four chromosomes (Lange et al. 1993; Oleo et al. 1993). More recently, a malate dehydrogenase isozyme tightly linked to root-knot nematode (*Meloidogyne* spp.) resistance has been described (Yu et al. 2001), and further developments have generated a cleaved amplified polymorphic sequence (CAPS) marker near this locus (Weiland and Yu 2003).

6.2 Construction of Genetic Maps

Isozyme and morphological markers were integrated with restriction fragment length polymorphic markers (RFLPs) using both anonymous and named DNA probes (Pillen et al. 1993). A number of genetic maps have been constructed with molecular markers (Barzen et al. 1992, 1995; Pillen et al. 1992, 1993; Uphoff and Wricke 1995; Halldén et al. 1996; Schondelmaier et al. 1996; Nilsson et al. 1997; Schumacher et al. 1997; Hansen et al. 1999; Rae et al. 2000). All but two maps (Yu 2004; Trebbi 2005) have been constructed from sugar beet and other crop types are not yet represented, although the fundamental genetic basis is unlikely to be much different, but allele frequencies likely vary and fixation of "crop use specific" alleles might be expected. Maps have been constructed using anonymous genomic restriction fragment length polymorphic (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphic (AFLP) markers, and simple sequence repeats (SSR), and where possible maps have included morphological and isozyme markers. Most SSR markers to date were developed in the private sector and their availability is restricted. Single nucleotide polymorphisms (SNP) are becoming available for mapping in sugar beet (Schneider et al. 2001; Möhring et al. 2004).

The number of markers ranged from 85 to 413 markers and the genetic distance summed across all nine linkage groups (corresponding to the basic chromosome number of nine in *Beta*) for each map ranged from 621 to 1,057 cM. The reason for a large difference in genetic map length is not clear, but it is not related to the number of markers mapped. Most maps have shown a strong clustering of markers in one or two regions of each linkage group, suggesting restricted

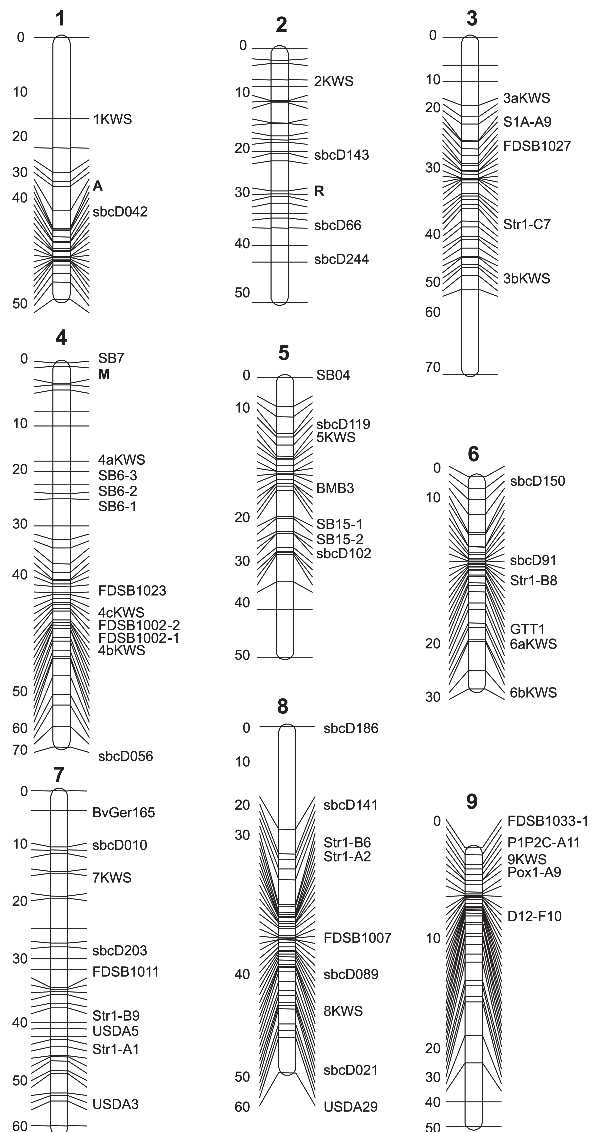

Fig. 1. Genetic map of *Beta vulgaris* (after Trebbi 2005). Chromosomes are numbered according to Schondelmaier and Jung (1997), using SSR markers previously assigned to linkage groups by KWS SAAT AG, Einbeck, Germany (*suffix KWS*). All other named markers except those with *single letter* designations are fragment length polymorphisms associated with cDNA clones. Single letter designations are morphological loci conferring nuclear male-sterility (*A*), red betalain pigment production (*R*), and multigerm seed (*M*). Not shown, but indicated with a *line* on each linkage group, are positions of scored AFLP markers. Total map length is 512 cM

genetic recombination but also arising from the type of marker used (Nilsson et al. 1997). Each of the genetic maps shows variation in the number of detected duplicated loci, ranging from less than 2% (Pillen et al. 1993) to over 38% (Barzen et al. 1995). Up to three bivalents have been detected in meiotic chromosome analyses of haploid sugar beets (Yu 1980; Cistue et al. 1985), suggesting some duplicated chromosome regions exist in beet. The map of Trebbi (2005) involved a cross between sugar beet and table beet using predominantly AFLP markers (Fig. 1), and Yu (2004) using similar markers mapped a sugar × wild beet population. Comparative genome analyses using *Arabidopsis* conserved genes were mapped in a number of species including beets with a conclusion that conserved synteny blocks extend among unrelated dicot plant families (Dominguez et al. 2003).

Particularly noteworthy is the work of Schondelmaier and Jung (1997) who defined molecular, isozyme, and morphological linkage groups based on the Butterfass (1964) trisomic series, thus establishing a common nomenclature for beet linkage groups. Inconsistencies persist in the literature regarding chromosome assignments, although many maps contain a few markers in common, such as the red color locus (*R*) or monogermity (*m*).

6.3 Gene Mapping and Marker-Assisted Selection

Genes for annual vs. biennial habit (*B*), restoration of cytoplasmic male-sterility (*X* and *Z*), nematode resistance, sugar yield, Cercospora leaf spot resistance, and rhizomania resistance have received considerable attention as a result of their considerable economic importance to the beet sugar industry.

In addition to linkage with and isozyme marker (Abe et al. 1993), the annual habit gene *B* was tightly flanked (ca. 5 cM) with RFLP markers (Boudry et al. 1994). AFLP markers were used to saturate this region, resulting in recovery of four markers within 1 cM or less, including two that showed no recombination with the bolting locus (El-Mezawy et al. 2002). A dense physical map has been constructed around this locus in preparation for map-based cloning (Hohmann et al. 2003).

Loci involved in restoration of male-fertility in a sterile cytoplasm, *X* and *Z*, have been located on Butterfass chromosomes 3 and 4, respectively (Schondelmaier and Jung 1997). Locus *X* was located terminally on chromosome 3 (Pillen et al. 1993; Uphhoff and Wricke 1995). A quantitative trait loci (QTL) approach to mapping restorer genes was taken by Hjerdin-Panagopoulos et al. (2002). Two QTLs, 15 cM apart and explaining 79% of the variability, were detected on chromosome 4, and in a different population, another QTL on chromosome 3 explained 72% of the phenotypic variance, and these QTLs likely correspond to *Z* and *X*, respectively, although which specific QTL on chromosome 4 relates to *Z* is uncertain.

Desplanque et al. (2000) characterized a number of mitochondrial types within wild beet populations, in addition to the commonly used Owen (1945) S- and N-cytotypes. Using bulked segregant analysis and AFLP markers, Touzet et al. (2004) described a novel restorer locus for the G-cytotype on chromosome 8. Previously, Laporte et al. (1998) demonstrated linkage of RAPD markers with monogermity (*m*) and a restorer for the H-cytotype, and suggested that this may not be novel since Owens gene *Z* and *m* are on Chromosome 4. Touzet and Budar (2004) describe some of the potential gene functions that could be implicated in CMS fertility restoration.

Marker analyses for corrected sugar yield and sugar content, as well as amino-nitrogen, sodium, and potassium, the primary solutes involved in loss of sucrose to molasses during processing, were performed in two segregating populations tested in a number of environments in order to identify QTLs associated with these characters (Weber et al. 2000). QTLs were discovered but they generally mapped in different chromosomal locations in the two populations and only a few were stably expressed in the same population across environments. Expressed sequence tags (ESTs) predicted to function in carbohydrate and nitrogen metabolism (e.g., candidate genes; Schneider et al. 1999), were used to map QTL for seven traits related to sugar production (Schneider et al. 2002), including corrected sugar yield, root yield, ion balance, sugar content, amino nitrogen, potassium, and sodium. Phenotypic evaluation was of test cross progeny grown in six locations. Twenty-one QTLs were detected for these traits, and four of these were found across different environments (root and corrected sugar yield located on chromosome 4, sucrose content on chromosome 9, and potassium level on chromosome 2). Trebbi and McGrath (2003) examined QTLs for sucrose content in a sugar beet by table beet cross (Trebbi 2005), with particular focus on su-

crose content as a proportion of dry matter content, and found 13 QTLs distributed throughout the beet genome.

Sugar beet cyst nematode resistance, morphological, and isozyme markers were placed on the maps of Wagner et al. (1992) and Uphoff and Wricke (1995). Resistance to the beet cyst nematode (*Heterodera schachtii*) is found among wild species of the section *Patellares*, and introgression into beets has been possible via chromosome translocation. At least three different resistance genes have been defined, i.e., *Hs1* in the homoeologous chromosomes 1 of the three species in this section, *Hs2* in the homoeologous groups to chromosome 7 of *B. procumbens* and *B. webbiana,* and *Hs3* in chromosome 8 of *B. webbiana* (Kleine et al. 1998). Species-specific DNA probes were used to identify wild chromosome segments containing *Hs1* in segregating progenies of monosomic alien addition lines (Schmidt et al. 1990; Jung and Hermann 1991; Jung et al. 1992; Salentjin et al. 1992). RAPD markers were also linked to resistant genes Hs^{pro-1} (Halldén et al. 1997) and Hs^{pat-1}, where two out of six markers were closely linked to the Hs^{pat-1} and one of them was converted to a sequence tagged site, usable for gene cloning (Salentjin et al. 1995). With the use of genome-specific satellite markers and chromosomal break-point analyses, the $Hs1^{pro-1}$ locus was positionally cloned (Cai et al. 1997) and redeployed by genetic transformation (e.g., Koenig and Buttner 2004) in the hopes the yield penalty shown by translocation stocks could be averted.

QTLs for Cercospora leaf spot resistance have been identified (Nilsson et al. 1999; Schafer-Pregl 1999; Setiawan et al. 2000; Weber et al. 2000), where five genes previously were implicated in its expression (Smith and Gaskill 1970). Five QTLs accounting for 7 to 18% of phenotypic variation each (based on 221 AFLPs and 46 RFLPs), located on linkage groups 1, 2, 9 and two on linkage group 3, were detected by composite interval mapping (Nilsson et al. 1999). Schafer-Pregl et al. (1999) analyzed QTLs under natural and artificial inoculation and repeated at different plant stages, where three major QTLs were detected on chromosomes 2, 6 and 9 in all conditions, and suggested three additional QTLs on chromosomes 4 and 5 in an F_2 population only. In artificial epiphytotics an additional QTL on chromosome 3 was seen. Setiawan et al. (2000) characterized four QTLs located to chromosomes 3, 4, 7 and 9.

Resistance to powdery mildew (*Erysiphe betae*) has been found in beet. Several QTLs for oligogenic resistance, explaining 27% of the phenotypic variance, have been identified. Monogenic resistance has also been described (Janssen et al. 2003).

Rhizomania is perhaps the most important recent disease of sugar beet, and marker-assisted selection has been instrumental in deploying resistance (Biancardi et al. 2002). Two resistances are known, derived from different sources, named *Rz1* and *Rz2* (Scholten and Lange 2000). Barzen et al. (1992) identified a RFLP marker linked to *Rz1* on chromosome 4, and subsequently sequenced RAPD markers to develop sequence characterized amplified region (SCAR) markers within 2 cM of the *Rz1* locus (Barzen et al. 1997). This locus was also described by Pelsy and Merdinoglu (1996) using bulked segregant analysis (BSA) to first identify linked RAPDs, mapping those in an F_2 population, and performing a QTL analysis that demonstrated ca. 67% of the phenotypic variance associated with a single region, and likely found by Giorio et al. (1997) in a different sugar beet accession. Discovery of *Rz2* and its linkage with *Rz1* was done with RAPD markers and subsequently converted to sequence tagged site (STS) markers, separated by a distance of ca. 20 cM on chromosome 4 (Scholten et al. 1997, 1999).

Disease resistance genes often show common nucleotide sequence motifs, and the general class of resistance genes (R genes) and their analogs (RGA) are of considerable interest. Hunger et al. (2003) used degenerate primers designed using R gene sequences to recover 47 genomic and cDNA RGAs showing expected motifs and domains for 21 nucleotide binding sites (NBS): leucine-rich repeat (LRR) R gene domains and 19 for serine (threonine) protein kinase domain R genes. RGAs were mapped to all chromosomes, identifying alleles associated with rhizomania and Cercospora resistance, within a cluster of nine RGAs on chromosome 7. Interestingly, neither Hunger et al. (2003) nor Tian et al. (2004) could recover any clones corresponding to the TIR-type R gene class in sugar beet, suggesting that beets have lost this particular type of R gene during its evolution.

6.4 Advanced Works

Over 22,000 *B. vulgaris* expressed sequence tags from beet are available and significant information is available on their putative functions. For

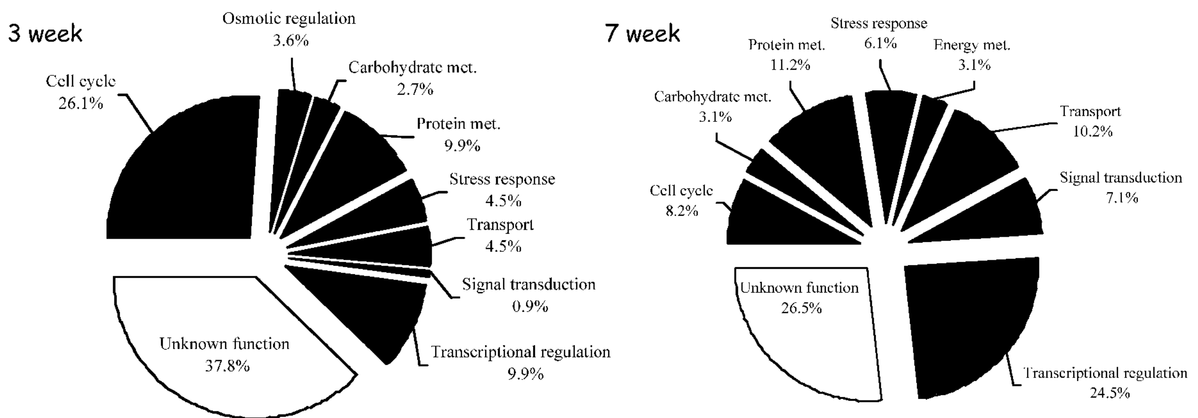

Fig. 2. Functional class distribution of sequences recovered from 3 and 7-week-old beet taproots. Note that 3 WAE (weeks after emergence) has a richer representation of cell cycle and osmotic regulation putative gene products, and 7 WAE functional categories are more highly represented in transport, signal transduction, and transcriptional regulation functional categories (Trebbi 2005)

instance, ESTs collapse into 12,950 tentative consensus (TC) sequences, representing 11,677 peptides (http://sputnik.btk.fi/). The database openSputnik is well-populated with physical characteristics (length, GC content, etc.), annotative attributes (developmental stage, tissue, clone library, etc.) and functional attributes (functional distribution, rankings, gene ontologies, etc.). A Michigan State University (MSU) website (http://genomics.msu.edu/sugarbeet/) contains static clustering and BLAST results against *Arabidopsis* and nonredundant nucleotide sequence space. Both databases are incomplete. The Sputnik database is geared towards comparative evolutionary genomics (Rudd 2005). All TCs have been assigned putative functions, where similarities are identified via BLAST, by comparing against the *Arabidopsis thaliana* genome sequence and/or the database of nonredundant sequences, and results were posted on public websites http://genomics.msu.edu/sugarbeet/, http://sputnik.btk.fi/ (accessed 04/04/2006). The majority of sequenced clones (ESTs) were preselected prior to sequencing to remove a large proportion of redundant transcripts, and thus represents a unigene set of over 10,000 uniquely expressed gene sequences covering four (young and mature roots, leaf, and flower) important developmental stages of beet growth (Herwig et al. 2002). Recently, The Institute for Genomic Research (TIGR) compiled a gene index of beets, resulting in a comprehensive functionally annotated resource of the available nucleotide sequence data (http://www.tigr.org/tdb/tgi/plant.shtml, accessed 04/04/2006).

Taproot specific ESTs were recovered by Kloos et al. (2002), and root EST macroarrays confirmed and extended these results (Bellin et al. 2002). Enzymes of the glyoxylate pathway, deduced through EST approaches, were expressed at high levels in stress germination environments (de los Reyes et al. 2003) as was a germin-like protein gene thought to be an oxalate oxidase providing germination-promoting hydrogen peroxide from seed reserves of oxalic acid (de los Reyes and McGrath 2003). Trebbi and McGrath (2003) examined differential gene expression analyses performed on root tissues sampled from the first to the ninth week after emergence (WAE) via 134 cDNA-AFLP primer and showed 1121 differences, suggesting a transition from juvenile to adult plant growth occurs at by 6 WEA. Analyses of 442 EST sequences obtained by subtractive hybridization supported this transition as some transcript classes were underrepresented at one of the two time points examined (Fig. 2).

6.5 Future Scope of Works

Beyond marker analyses of traditionally important agronomic and disease traits, which needs to continue and expand, further insight into the growth and development of the beet including differences between crop types as well as the responses beets exhibit towards the environment, will need increased attention. Early season growth (e.g., the first 10 weeks) is a critical phase of the beet's life, not only to have good field stands but also to acquire metabolic capacity for agronomic productivity. Early season development includes acquisition of disease resistance (from acute symptoms

with devastating effects to chronic symptoms that reduce yield potential), and development of the taproot. This change from seedling to adult vegetative growth coincides, in the field, with warming temperatures (and greater seedling disease), increased growth rate, and increased light interception. Yield of sucrose is directly proportional to the interception of solar irradiation, and maximal interception of sunlight does not occur until the crop canopy is fully developed usually past the summer solstice. Critical insight into gene expression during early growth will help increase biomass production and reduce seedling mortality. Most (if not all) constructive agronomic processes are in place by the tenth week after emergence. Disease losses are a constant concern through the growing season and during postharvest storage, but are caused by a relatively small number of pathogens for which genetic resistance is generally available.

Transition to adult growth is a new concept, for beets, where there are at least two developmental phenotypes associated with a transition; development of supernumerary cortical rings by at least three weeks postgermination, and the sharp increase in sucrose content occurring roughly between four and seven weeks after germination. Whether these disparate phenomena constitute a developmental phase shift between juvenile and adult plant growth is speculative, but clearly a number of developmental events must happen that allow the beet taproot to act as a mature storage organ.

Integrating gene discovery with sugar beet breeding will result in a set of annotated genes useful for recognition and prediction of beet development and response to environment, including challenges associated with biotic and abiotic stresses. Such knowledge ultimately could be used to manipulate biochemical pathways to maximize beet agronomic and horticultural performance. Basic knowledge about the range of biochemical functions as well as their tissue localizations and genetic contributions will allow development of rational molecular breeding objectives.

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