Chapter 12

DROUGHT ADAPTIVE TRAITS FOR SUGAR BEET IMPROVEMENT

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INTRODUCTION

Sugar beet is one of the more important field crops, traditionally cultivated as a vegetable, but mainly for sugar extraction. In recent years, sugar beet has also been considered as a potential source for ethanol production (Keil et al., 2009). The crop is currently grown on more than 5 million ha, across 52 countries of Europe, Asia, America, and Africa. With an average of 147 Mt produced annually, sugar beet provides about 20% of world sugar production (FAO, 2009). The rest is extracted from cane (Saccharum officinarum L.). While sugar cane is a tropical/sub-tropical crop, much of the sugar beet cultivation is in temperate areas of the northern hemisphere, between 30-40 and 60°N (Draycott and Christenson, 2003; Leff et al., 2004). The main world producer is the European Union, with around 67% of total sugar beet production. The crop is grown in a wide range of climates, and in the last decades it has also extended to subtropical regions.

Sugar beet belongs to the genus Beta and species vulgaris, which is divided into three subspecies (ssp.): vulgaris, maritima, and adanensis. The ssp. vulgaris includes the cultivated varieties: leaf beets, garden beets, fodder beets and sugar beets. According to Lange et al. (1999), sugar beet is classified as Beta vulgaris L. ssp. vulgaris L. (Sugar Beet Group). The genus Beta belongs to the Amaranthaceae (formerly Chenopodiaceae) family.

The common ancestral progenitor has been identified as sea beet (Beta vulgaris L. ssp. maritima (L.) Arcang), still widespread on Mediterranean and Atlantic seashores from Norway to north-central Africa. Its geographical origin is believed to be the coastal regions of Asia Minor (Coons, 1949, 1954). It is presumed that domestication of sea beet began around to 8,500 BC in the Persian Gulf region (Zohary and Hopf, 2000), and that leaf beets were
commonly grown for their leaves in the 9th century BC in Greece, Syria and Persia. Varieties with edible roots probably appeared at the time of the Roman Empire, while varieties were developed during the Middle Ages that had large roots suitable for cattle feed (reviewed by Biancardi, 2005). Beet for sugar production is the more recent application (Coons, 1949, 1954). It began being cultivated in Northern Europe in the early 19th century, when the first beet variety was selected for sugar processing. The White Silesian Beet was developed at the end of the 18th century by Karl Achard, likely through mass selection of fodder beets (Fischer, 1989).

Since then, yield gains in sugar beet have benefited from continuous and combined advances both in selection and in crop practices (Jaggard et al., 2007). Demand by growers and sugar factories for high yields have led to the development of new varieties with improved traits, not only for yield and high sugar content, but also for the processing quality parameters (low levels of impurities, etc.) on which the rate of sugar extraction depends (Campbell, 2005). Breeders’ efforts were also focused on improvement for yield stability (Campbell and Kern, 1982; Frese et al., 2001). Within this objective, the introduction of varieties with wide adaptability for specific environments and resistance to pests and diseases has been of primary importance since the mid-20th century (Frese et al., 2001). The introduction of hybrid varieties, monogermity, some disease resistances, meristem multiplication techniques, and breeding assisted by molecular biology etc., have provided other major genetic contributions to the sugar beet yield increase over the last 50 years (Savitsky, 1940; Owen, 1945; Biancardi, 2005).

Relative genetic vs. agronomic contributions to yield improvement have been estimated at about 50% (Sneep et al., 1979). At present, the average sugar content of modern commercial varieties is 16-20%. Indeed, it is estimated that sugar contents of standard commercial hybrids have improved from 4-8% in the mid-18th century (Draycott, 2006). However, at spatial level and to a lesser extent, on a temporal scale, sugar beet average yields are highly variable, due to the high genotype - environment (G*E) interaction. It is well recognized that pedoclimatic factors have a major influence on plant growth and productivity (Boyer, 1982). The effects of severe environmental conditions have been shown to be responsible, more than pests and diseases, for the difference between the real and theoretical field production of the major crops.

Water shortage is a global issue as primary crop yield limiting factor. In sugar beet, water stress is the main critical cause affecting its economic viability, limiting both yield and processing quality and increasing production costs (Berbel and Gomez-Limon, 2000; Hoffmann et al., 2009).

Following expansion of the beet-growing area from central Europe to a wider range of agroclimatic conditions, varieties which need different sowing dates have been introduced on the basis of the best match of plant seasonal growth and development patterns with local rainfall and temperature. However, about 20% of sugar beet is currently grown under irrigation in order to ensure profitable yield performance. In warm and dry regions like Southern Europe, North Africa and Western US, sugar beet is usually sown in autumn and harvested in summer, around one month earlier than the traditional crop (Rinaldi and Vonella, 2006). Winter or spring sowing is also possible in these areas, but sugar yield is more likely to be reduced. In addition, the requirement for irrigation is higher than with autumn-sown varieties, which may benefit from more frequent rainfall and lower evapotranspiration due to the anticipated harvest as well (Campbell, 2002). Autumn-sown crops also benefit from a
deeper and better developed root system. Nonetheless, supplementary water is normally needed before harvest (Tognetti et al., 2003).

In northern temperate zones, sugar beet is typically sown in spring and harvested in autumn. In these areas (Northern Europe, Eastern US regions including Michigan, Red River Valley in Minnesota, and North Dakota), sugar beet is typically grown under rainfed conditions, with irrigation only being used to supplement inadequate precipitations in very dry years or in specific locations (Pidgeon et al., 2001). Under these growing conditions, low solar radiation and temperature, rather than lack of water availability, has been regarded as the major constraint to sugar beet yield (Wareing et al., 1977).

Recent studies have also pointed out the increasing importance of sub-optimal water availability in yield losses in the East of England, Eastern Germany and Western Poland (Jones et al., 2003). Under global climate change, the impact of adverse environmental events associated with water stress, such as drought, high temperature, high level of solar radiation and evapotranspiration, low soil moisture and fertility etc., is expected to intensify in many areas. Sugar beet yield losses due to water shortages are therefore predicted to become more severe in Southern, Western and Central Europe (Jones et al., 2003). While available water resources for agriculture consumption are declining, concerns about the potential impact of climate change on crop yield and associated production costs raise the question of the future economic sustainability of the sugar beet crop. For many areas, and especially in irrigated spring-sown sugar beet, it is recognized that this will depend mainly on the enhancement of yield stability under water-limited conditions, at the same time reducing irrigation inputs which are becoming economically and environmentally less sustainable (Steinrücken, 2005).

For this purpose, high-efficiency water use is a crucial line of research. Efforts aimed at improved water use should include the implementation of more innovative irrigation techniques, appropriate cropping practices, and proper timing and rates of water applications (Davidoff and Hanks, 1989). For instance, studies on sugar beet yield response to different irrigation intensities have recognized the feasibility of reducing the levels currently used, since satisfactory crop yield is not compromised under controlled deficit irrigation management (Winter, 1980).

At the end of the vegetative stage, moderate water stress reduces root development, but increases sugar concentration which improves the processing quality. On the other hand, over-irrigation can produce detrimental effects on yield performance by increasing the occurrence of pests and diseases, nutrient leaching, and reducing sugar concentration (Harveson and Rush, 2002). An attractive and promising strategy for enhancing water use efficiency is the selection for water stress tolerance, aimed at developing genotypes with better adaptation under sub-optimal water conditions (Rajabi et al., 2009).

**WATER DEMAND AND WATER DEFICIT**

Sugar beet is considered a high water-consuming crop. In general, this concept refers to the water requirements in relation to balancing water losses through evapotranspiration (ET), i.e. leaf transpiration plus soil evaporation (Allen et al., 1998). Major factors affecting ET are: i) climate and weather conditions (rainfall, solar radiation, temperature, wind, air humidity, etc.); ii) soil traits (texture, waterholding capacity, drainage etc.); iii) cropping practices
(sowing date and harvest schedules, irrigation systems, amendments, etc.); iv) crop characteristics and growth stage (Debaeke and Aboudrare, 2004).

In sugar beet, maximum sugar yield requires approximately 550 to 750 mm of water regularly distributed from sowing to harvest, which is in any case 50% less than sugar cane (Mrini et al., 2001). However, the magnitude of total and daily ET is extremely variable, being significantly higher under dry and warm conditions, and in the mid-growing season. Studies on crop water requirements have provided evidence about the pronounced correlation between ET and growth patterns over the life cycle. The size and shape of the canopy, leaves, and root are thought to be particularly influenced (Werker and Jaggard, 1998).

**WATER STRESS EFFECTS**

The magnitude of water deficit injuries on plant growth and development and on final yield performance is determined by a wide range of factors, including the timing, duration and intensity of the stress in relation to the crop growth stage and seasonal water demand (Owen, 1958). Early in the growing season, sugar beet is known to be very susceptible to moisture deficits. Water stress during the germination and emergence stages can affect the optimal stand (around 80-100,000 plants ha\(^{-1}\)) and early growth, which substantially reduce the sugar yield (Carter et al., 1980; Brown et al., 1987). On the contrary, later in the season, the crop is reported to be a drought tolerant species (Choluj et al., 2004). This is partly because sugar beet can develop a deep root system, which allows the plant to uptake water stored in the deep soil (Vamerali et al., 2009).

The crop displays water stress symptoms when the rate of loss by ET exceeds the amount of water available for root uptake from rainfall, irrigation and soil moisture. Adaptive mechanisms for drought tolerance are: i) stress escape, ii) stress tolerance, iii) stress avoidance (Levitt, 1972); other authors also include stress recovery (O'Toole and Chang, 1979). The effects of water stress occur primarily in the leaves. Minimal decreases in leaf water potential are enough to reduce regular development of the leaf apparatus. Water stress leads to a reduction in Leaf Appearance Rate (LAR) and Leaf Area Index (LAI) and, consequently, the interception of light radiation. An 84% decrease in the leaf area of sugar beet subjected to drought stress has been observed by Abdollahian-Noghabi and Froud-Williams (1998). The growth of new leaves is less sensitive to water deficit than the expansion of already formed leaves. The negative effect of water stress on leaf development might be partly explained by the reduced uptake of soil nutrients. Indeed, low water availability reduces the movement of ions to the root, generating large fluctuations of nutrients in the plant and, as a consequence, nutritional deficiency (Carter et al., 1980). According to Ober and Luterbacher (2002), there are genotypic differences in the sensitivity of leaf expansion to drought.

Water stress can strongly diminish leaf water potential and stomata conductance (Lawlor and Milford, 1975). This limits photosynthesis by decreasing not only carbon dioxide exchanges, but also leaf cooling, which causes the insurgence of heat stress that can damage leaves and accelerate their senescence. The stomata are very sensitive to changes in soil water status and normally tend to close with a decrease in soil water potential from 5 to 15 bars (Milford and Lawlor, 1976). In this range, the stomatal conductance of young leaves is almost
three times greater than that of older ones. This difference in stomata behavior means less efficient use of water as the young leaves continue to transpire, even after the closure of the stomata in mature leaves. Stomatal conductivity is related to the soil water status through abscisic acid (ABA), a plant hormone that acts as a signal in root-leaf communication. Stomata guard cells have specific receptors for ABA, located on the external surface of their cell membranes. ABA contributes to the regulation of stomata opening through the modulation of ion channels and proton pump activity (Zeevart and Creelman, 1988). Stomatal closure is associated with the inhibition of carbon dioxide uptake and nutrient flow from the roots. The "low stomatal density" trait seems to be correlated with tolerance to water stress in sugar beet (Thomas and Clarke, 1995). Nevertheless, selection for fewer stomata might lead to a reduction in sugar yield, due to the positive association between the traits. Other anatomical characteristics of the cuticle and epidermis in sugar beet could be considered as efficient indicators of drought tolerance. For instance, an increase in wax content might be used to improve drought tolerance and water use efficiency (Luković et al., 2009).

Plants accumulate solutes in a process called "osmotic adjustment". In older leaves, proline, sucrose, and betaine play a dominant role, but in younger leaves the same process depends only on betaine and sucrose. The decrease in cellular potential increases the driving force for water uptake and counteracts loss of turgor or salinity stress. The principal solutes are sucrose, betaine, proline and inorganic ions, such as sodium. Sugar beet genotypes differ in osmotic adjustment, but it is unclear if this trait contributes to improving yield under drought conditions. The effective mechanism for osmotic adjustment, both in the shoot and root tissues, may be critical to survival rather than to maintain plant growth (Serraj and Sinclair, 2002). Drought treatment in a greenhouse causes a significant increase of betaine content, especially in the young leaves.

The accumulation of amino acids in response to osmotic stress is well known (Rontein et al., 2002). According to these authors, under sufficient water supply the concentrations of betaine and amino N were almost the same. However, under severe drought, amino N increased fourfold, whereas betaine only increased twofold. The higher rise in unspecific amino acid relative to betaine concentrations probably reflects the build-up of metabolites as a result of impaired growth, rather than specific osmotic adaptation. It seems that betaine is a more effective osmolyte in sugar beet leaf tissue than proline. Shaw et al. (2002) demonstrated that a putative drought tolerant sugar beet genotype reacted to water deficiency by raising its betaine level in the shoot, but also between 2.5- and 4-fold in the roots. Hanson and Wyse (1982) observed that betaine concentrations in the shoots of five different unsalinized and salinized sugar beet genotypes were closely correlated with the value of leaf osmotic potential. Ghoulam et al. (2002) concluded that betaine played the main role in osmotic adjustment in sugar beet plants under osmotic stress. The high level of betaine could mask the contribution of other nitrogen components in osmotic response (McCue and Hanson, 1992).

Increased concentrations of soluble N under drought conditions could be an effect of inhibited growth and reduced utilization of low-molecular N components for protein synthesis (Hanson and Hitz, 1982). Among the nitrogen compounds, nitrate increased up to 9-fold when plants were subjected to severe drought. High nitrate concentrations under water deficiency can be due to a decline in nitrate reductase activity when plant water status is lowered (Hanson and Hitz, 1982). Gzik (1996) demonstrated a marked increase of proline in sugar beet leaf discs exposed to dry air. After periodic or permanent soil water stress, a 5-fold
increase of proline level in sugar beet leaves was reported by Rover and Buttner (1999). Salinity induced an increase in proline concentration in leaves of five varieties of sugar beet (Ghoulam et al., 2002). The authors concluded that the response was positively correlated with the level of salt tolerance, although, from a quantitative point of view, the true contribution of the increased proline concentrations to osmotic adjustment appeared to be weak. The accumulation of soluble sugars in plants as a response to water deficit is also quite well documented and is considered to play an important role in osmotic adjustment (Hare et al., 1998).

**ROOT APPARATUS AND WATER STRESS**

Sugar beet can be considered a model plant for root studies because it has a more developed and deeper root system than most other crops. Measurements taken by different authors refer to a maximum depth of 2.5 m (Girard, 1885), 2.1 m (Andrews, 1927), 2.8 m (Märländer and Windt, 1996), and 2.74 m (Winter, 1998). This gives sugar beet roots the ability to uptake significant amounts of water and nutrients from the deeper soil layers, thus limiting the effects of stress (Stevanato et al., 2010). Indeed, sugar beet shows the highest root water uptake from the deeper root zone under sub-optimal water supplies (Brown et al., 1987). Sugar beet compensates its relatively lower mean root length density (RLD) by having a higher rate of water uptake: up to five times that recorded for winter wheat (Brown and Biscoe, 1985). As reported by Peterson et al. (1979) in Nebraska, sugar beet can absorb labeled nitrogen (\(^{15}\)N) from a soil depth of up to 2.40 m. Surveys conducted in Italy recently confirmed that the crop can uptake nitrogen as ammonia to a depth of 3 m (Stevanato et al., 2010). These studies emphasize the direct influence of water and nutrient availability on the root architecture of sugar beet.

Drought stress greatly reduces the total dry matter yield of the crop. It also consistently increased the concentration of α-amino-N compounds, betaine and proline, along with sodium and potassium (Gzik, 1996). These are the principal impurities that reduce sugar beet quality for processing by inhibiting crystallization at the end of the industrial process. Drought thus negatively affects not only yield, but also the rate of sugar extraction. Although all these components reduce the percentage of sugar that can be extracted, the formulas employed in sugar factories for losses assessment only consider potassium, sodium, α-amino N (which represents only a variable percentage of the soluble N compounds) and reducing sugars (Buchholz et al., 1995).

There is an appreciable genetic variation in sugar beet for the concentration of sucrose and other solutes in the taproot, but information is scarce on the variability in the accumulation of solutes under drought conditions. Solute accumulation under drought can point to osmotic adaptation, which may be linked to the stress sensitivity of the crop. Increased concentrations of soluble N under drought could be an effect of inhibited growth and reduced utilization of low-molecular N components for protein synthesis. However, increases in pool size of nitrogen metabolites can also have adaptive significance (Hanson and Hitz, 1982). Among the nitrogen components of the roots, betaine is quantitatively more important. Betaine is considered as a non-toxic osmoticum, which is accumulated in the cytoplasm in response to decreased vacuole water potential. The accumulation of amino acids
in response to osmotic stress is well known and is also attributed to their capacity as compatible solutes (Ronstein et al., 2002). Proline accumulation in sugar beet roots can be considered both as a stress indicator, and as a nitrogen compound that reduces the quality of the root. Both stressful conditions and excess N lead to mobilization of stored carbohydrates to supply energy and carbon skeletons to synthesize stress molecules and N containing substances, diminishing sucrose yield and decreasing the quality of the root.

**Breeding for Drought Tolerance: The Role of Wild Beet Germplasm**

The genetic base of modern varieties has remained quite unchanged from the early sugar genotypes selected in central Europe under temperate conditions and relatively free from stress and diseases. Indeed, faced with the need for drought-resistant varieties, and in general for reducing yield losses under abiotic stresses, the advisability of broadening the genetic variability within the commercial gene pool has received increasing attention. The genetic variability is very narrow if compared with the wild beets germplasm (Jung et al., 1993). Current sugar beet varieties are the outcome of around 200 years of selection and breeding improvements, also resulting from crossing programs between cultivated and wild beets. From pioneering works in the early 20th century (Munerati, 1920), intraspecific hybridization between wild and cultivated beets provided breeders the opportunity to introduce essential genetic resistance against severe diseases, such as cercospora leaf spot and rhizomania (Biancardi et al., 2002), into the commercial gene pool. Nevertheless, until the 1980s, breeders were reluctant to exploit the related wild and other cultivated germplasm (leaf, garden and fodder beets) because of a number of undesirable traits associated with introgression of resistance genes (Panella and Lewellen, 2007). Not unlike in other crops, genetic improvement of sugar beet has been based on the utilization of the primary gene pool because such material can at least be easily crossed with elite lines (Francis and Luterbacher, 2003). According to Maxted et al. (2006), the primary gene pool of sugar beet includes the cultivated forms (GP-1A) and the wild (sea beet) or weedy forms of the crop (GP-1B).

As discussed above, conventional breeding programs have contributed substantially to yield improvement over the last half century. However, it is argued that yield gains attainable with standard selection methods and using the available germplasm have reached a limit beyond which any further improvement will be quite difficult. An attractive strategy to increase sugar production is to reduce yield losses due to biotic and abiotic stresses. Supplementary yield gains under water and nutrient stresses could depend on the enlargement of the genetic basis of the current sugar beet germplasm. Sea beet is known to have a high resistance to abiotic stresses, such as salinity and low water availability, and that there is wide genetic variability within sea beet populations. Nevertheless, there is no evidence of successful transfer of drought stress tolerance in the gene pool of modern varieties. Recent screening techniques based on molecular marker analysis have confirmed that modern sugar beet varieties only encompass a quarter to a third of the genetic variability present in wild populations (Saccomani et al., 2009). Reduced variability has resulted from the introduction of cytoplasmic male sterility and monogermity in commercial seed (McGrath, 1999).
Genotypes screening for drought tolerance provides an opportunity to broaden the genetic diversity within the primary breeding pools (Panella and Lewellen, 2007).

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