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1 Introduction

Water in plant production

Water is in many ways essentially connected with plant life (EHLERS & GOSS 2003). Roots, stems and leaves of herbaceous plants consist to a major proportion of water, but plant dry matter synthesis involves water as well: As a hydrogen donor it is part of carbohydrates, which are synthesized by plants by the use of sunlight. A second anorganic compound for carbohydrate synthesis is carbon dioxide. CO_2 uptake through leaf stomata functions only via exchange with water vapour and therefore requires also a continuous supply of water. Water confers shape and solidity to plant tissues and is an important chemical agent in many chemical reactions. It is a solvent for salts and molecules and mediates chemical reactions, functions as a transport means for salts, assimilates and hormones within the plant and is necessary for cell enlargement and regulation of leaf temperature.

Lack of water has been a major selective force in plant evolution, and ability to cope with water deficits is an important determinant of natural distribution of plants and of crop distribution and productivity (FISCHER & TURNER 1978). Plant adaptions to such environments can be expressed at four levels: phenological or developmental, morphological, physiological and metabolic (HANSON 1980). An example for phenogical adaption is an extremely rapid completion of ontogeny. Morphological characteristics of adaption to a dry environment include deep rooting or special anatomical features of the leaves like wax coating over the cuticle, leaf shedding or leaf rolling. Regulation of stomatal conductance to water vapour is an example for a physiological adaption mechanism to drought. Adaption mechanisms on the metabolic or biochemical level are the least known and understood (HANSON & HITZ 1982). Metabolic responses of plants to water deficit can be stress-induced disfunctions but also potentially adaptive changes that reflect ordered operation of metabolic regulatory mechanisms. Among the latter is osmotic adjustment, an active mechanism of solute accumulation in response to water stress, leading to maintenance of turgor potential and hence continued plant growth (MORGAN 1984).

Meeting the needs for water has its limitations in crop production. Rainfall is one of the most important determinants for yield in many regions of the earth (HEINZOG 2003), including subhumid areas of the temperate zones where latent water

deficiency due to a deficit in the climatic water balance reduces yield potential. The traditional solution to agricultural water shortage is irrigation (BOYER 1996). A steady supply of water makes agriculture possible in many otherwise non-productive areas and the water often can bring reliable, high productivity. Because production becomes more predictable, investment can be made in other favourable cropping practices that result in further improvements in productivity. A major share of the global production comes from irrigated farms. However, supplies of water have become scarce as municipalities and environmental needs compete for the same water. As a consequence, installing new irrigation facilities is becoming less possible than in the past and there is increasing interest in improving the efficiency of water use and determining whether plants can yield well under water deficient conditions (BOYER 1982). A number of methods exists for improving the efficiency of water use which have been summarized by STEWART and NIELSEN (1990). The methods can be classified in three broad categories: (1) increasing the efficiency of water delivery and the timing of water application, (2) increasing the efficiency of water use by the plants, and (3) increasing the drought tolerance of the plants. According to HERZOG (2003) there is still a large potential for improvements in productivity per unit of water delivered to the farm by means of process engineering. But (1) includes also agronomic measures of soil water management and crop management as summarized by EHLERS and GOSS (2003), e.g. soil cultivation measures to control infiltration and evaporation and increase the quantity of extractable soil water, aspects of crop rotation, seeding date, stand density and fertilization.

Besides measures of process engineering and crop husbandry, improvements in the efficiency of water use can also be the basis of a breeding-oriented strategy. HERZOG (2003) mentioned three different components of water-use efficiency of a crop: A high efficiency of water uptake can be realized by deep, intensive rooting, which can be stimulated by agronomic measures or improved by means of breeding. Differences between species for evapotranspiration efficiency are well-known, genotypic variability, in contrast, only to a less extent, as its determination is methodically difficult. Improvements in harvest index allow for noticeable contributions to a more efficient water use only in crop species which have not yet been intensively worked on by breeding methods.

However, crop improvement under conditions of limited water supply involves more than water-use efficiency. Plants showing improved growth with limited water

availability are considered to tolerate drought regardless of how the improvement occurs. Effects like drought avoidance, postponing dehydration and dehydration tolerance are generally distinct from the factors controlling water-use efficiency (BOYER 1996). Of these three forms of drought tolerance, dehydration tolerance is most interesting because it often requires only slight repartitioning of dry mass. An example is osmotic adjustment, where the increased concentration of solutes can remarkably increase the ability of the cells to extract water from the soil.

Adaptability to drought in sugar beet

Sugar beet (*Beta vulgaris* L.) is an important crop grown throughout Europe, Asia and America, and global sugar beet production is 265 million tons per year. Sugar beet is one of the most productive crops in temperate climates (AZAM-ALI et al. 1994), but with a high demand for water, particularly during the main growth phase from June to September. Its total requirement for water is approximately 600 mm. Sugar beet can be classified as well adapted to drought in comparison to other spring sown crops with a comparable demand for vegetation period like field pea or potato (MCKERSIE & LESHEM 1994). The chenopod sugar beet originates from *Beta maritima*. Modern cultivated varieties of sugar beet are so closely related to the wild maritime form that they can be regarded as the same species (FORD-LLOYD 1986). *Beta maritima* colonises saline environments and has evolved specialised mechanisms to combat water deficiency stress. As a halophyte it belongs to the sodium includers (MARSCHNER 1995), which achieve osmotic adjustment by the accumulation of salts (mainly NaCl) in the cell vacuoles. This may be the underlying reason that sugar beet survives salinity and drought better than many other field crops. With regard to salinity, only cotton and barley are more tolerant (CLARKE et al. 1993). Moreover, sugar beet uses water rather efficiently (EHLERS & GOSS 2003) and there is no sensitive flowering stage during its long vegetative growth phase (DUNHAM 1993). It has a deep root system which enables it to utilise extensive volumes of soil water (WINDT & MARLANDER 1994). However, the plant shows apparently poor control of its internal water supply. The ability to regulate transpiration is very limited in sugar beet (HANSON & HITZ 1982) and wilting of leaves occurs frequently under conditions of high evaporative demand, even when water is readily available to the roots (MILFORD & LAWLOR 1975). The ability of the plant to compensate for decreasing soil water potential is limited and leaf water potential tends to decrease faster than soil water potential as the soil dries (LAWLOR & MILFORD 1975).

Annual precipitation and its distribution represent the main limiting factor for sugar beet growth in many regions. Particularly during the long summer season water supply is often insufficient. In dry regions, such as California or southern Europe, the crop is grown under irrigation. However, in other beet production areas where irrigation is not normally applied, such as the UK and parts of Germany, summer rainfall amounts are unpredictable and are usually insufficient to meet the crop's water requirements (OBEH & LUTEHBACHER 2002). In the UK, the impact of drought has been recognized as a major cause for yield losses in sugar beet (JAGGARD et al. 1998, PIDGEON et al. 2001) and averaged nationally for the UK, annual drought-induced yield losses were estimated to be 10 % of potential production, and rose to 30 % in drier years (JAGGARD et al. 1998). For continental Europe, similar figures can be assumed. E.g. in the year of 2003 with amounts of precipitation being far below average, white sugar yield was reduced to 28 % in some regions of Germany in comparison to the year of 2002 with steady water supply throughout the vegetation period. Additionally, water shortage is responsible for significant quality losses in sugar beet (BAGATTA et al. 2004). Technical quality of the storage root is determined by the concentration of soluble constituents like potassium, sodium, amino acids, betaine and further nitrogenous compounds which cannot be eliminated during processing and increase the amount of sucrose lost to molasses (HARVEY & DUTTON 1993, BURBA 1996). Drought-induced increases in the concentration of beet constituents reducing sugar extraction efficiency have been reported for potassium (ROVER & BUTTNER 1999, WINTER 1989) sodium (VAN DER BEEK & HOUTVAN 1993, ROVER & BUTTNER 1999), amino nitrogen (VAN DER BEEK & HOUTMAN 1993, CLOVER et al. 1999, KENTER 2003, ROVER & BUTTNER 1999, WINTER 1989), glycine betaine (CLARKE et al. 1993, KOCH et al. 1985, ROVER & BUTTNER 1999, SHAW et al. 2002, ŠVACHULA & PULKRÁBEK 2000) and proline (GZIK 1996).

The adaptability to drought has not been a breeding priority in sugar beet until now. In 1993 different commercial varieties of sugar beet were found to respond identically to drought/heat stress followed by regrowth of the crop (VAN DER BEEK & HOUTMAN 1993). However, genotypic differences for drought tolerance have been reported based on relative susceptibility for wilting in the field and on a regression analysis of relative sugar yield with the coefficient of varation for the experiment (CLARKE et al. 1993). These differences could in part be related to differences in the sensitivity of chlorophyll fluorescence as a measure of photosynthetic efficiency. ARSENIJEVIC-

MAKSIMOVIC et al. (2002) determined parameters of chlorophyll fluorescence, number of stomata, transpiration intensity, water potential of stem vessels, stomatal diffuse resistance, concentration of vessel solution and free proline content in leaves of eight different sugar beet genotypes. All parameters were modified under water deficit and genotypic differences in drought tolerance were described, but it was not possible to establish a general rule which would serve as a unique criterion for evaluation of sugar beet drought tolerance. ŠTAJNER et al. (1995) also attempted to relate adaptability to drought in sugar beet cultivars to differences in metabolical pathways. The activities of superoxide dismutase and peroxidase as important antioxidant enzymes protecting plants from lipid peroxidation and damage to all cell constituents were found to be decreased under drought stress in sensitive cultivars, whereas in tolerant cultivars activities mostly increased. Biochemical changes in sugar beet lines in dependence on soil moisture have been investigated by KEVRESAN et al. (1997/98) and differences occurred in the response of leaf water potential, net photosynthetic rate, RNA and DNA content, carbonic anhydrase activity, RUBISCO protein proportion and soluble protein content under stress. ABDOLLAHIAN-NOGHABI and FROUD-WILLIAMS (1998) screened sugar beet cultivars of different ploidy level and contrasting growth habit under different watering regimes in the greenhouse. The interaction between watering regime and cultivar was significant for both total dry matter and root dry weight, suggesting that there are beet cultivars relatively tolerant to drought stress. In recent work, 49 diverse sugar beet breeding lines were evaluated under adequate water supply and two levels of drought stress (SADEGHIAN et al. 2000) and exhibited large differential responses to drought for root yield and sugar yield. ORFER and LUTERBACHER (2002) assessed the degree of genotypic variation for drought tolerance within a wide range of sugar beet germplasm and genebank accessions within *Beta* and identified drought tolerant and sensitive lines in terms of yield reduction in polythene-covered vs. irrigated plots. Significant genotype x water treatment interactions were found for dry matter yield and relative leaf expansion rate. Significant genotypic variation occurred also for wilting score, rates of water use, osmotic adjustment and stomatal conductance and the percentage loss in biomass production due to drought was significantly correlated with specific leaf weight, leaf succulence index, water use and percentage green crop cover (ÖRER et al. 2004). A transgenic approach to improve drought stress resistance has been the introduction of fructan biosynthesis in sugar beet (PILON-SMITS et al.

1999). Transgenic lines of fructan-producing sugar beets showed significantly better growth under drought stress than untransformed beets.

Objectives

The present study aimed at investigating the performance of sugar beet under conditions of sufficient water supply and under drought stress of different severity. Yield response was related to changes in morphological, physiological and metabolic parameters of the plant. Special emphasis was placed on genotypic variability in the response to water deficiency. The genotypes included in the study had contrasting properties, representing the variability which exists in commercial sugar beet varieties at present. With regard to drought tolerance they comprised the largest possible variation which is available from European Breeders at the time. The particular objectives were as follows.

Which timeframe in ontogenesis is crucial for genotypic differences in field grown sugar beet to emerge? Are there interactions between genotype and harvest date? Is there genetic variability in the response to drought stress with regard to yield and quality parameters? (Section II)

What is the impact of water supply on dry matter production, gas exchange, chlorophyll fluorescence, water-use efficiency and carbon isotope discrimination of sugar beet? What is the relationship between water-use efficiency and carbon isotope discrimination in different sugar beet organs? Are there genotypic differences for parameters of gas exchange, chlorophyll fluorescence or water-use efficiency and do interactions with water supply occur? (Section III)

What is the effect of water supply on the chemical composition of the sugar beet taproot? Are there quantitative differences in the accumulation of various solutes? In how far are changes in solute concentrations reversible after stress relief? Are there genotypic differences in solute accumulation under drought and which are the implications for drought stress tolerance? (Section IV)

Results

In section **II** of this work "Seasonal development of genotypic differences in sugar beet (*Beta vulgaris* L.) and their interaction with water supply" growth and quality of different sugar beet genotypes were studied during the vegetation period. Possible interactions between the effects of genotype and environment were of particular

interest. Water supply as an important single determinant of the environment was studied separately analysing data from selected locations. Different sugar beet genotypes exhibited significant variability for taproot and leaf yield, taproot-to-leaf ratio and the concentrations of sucrose, potassium, sodium and α-amino N in the taproot. Differences existed already in mid June and virtually did not change any more from this time on. Accordingly, interactions between genotype and harvest date did not occur. Under drought conditions, withholding irrigation reduced leaf and taproot growth and taproot-to-leaf ratio, decreased the percentage of sucrose in dry matter and resulted in an accumulation of α-amino N. Interactions between genotype and water supply did not occur for any of the parameters studied.

In section III entitled "Impact of water supply on photosynthesis, water use and carbon isotope discrimination of sugar beet genotypes" the effects of drought stress on physiological processes in sugar beet were investigated. While gas exchange was clearly affected already under moderate drought, effective quantum yield of photochemical energy conversion was impaired only under severe drought. ^{13}C discrimination (Δ) was higher in leaf than in taproot and up to 2.4 parts per thousand lower in drought-stressed plants than in plants sufficiently supplied with water. This reduction in Δ corresponded to about 24 % higher water-use efficiency (WUE) in the drought stressed plants. Differentiating between plant organs, only leaf Δ was negatively correlated with WUE, whereas taproot Δ and WUE- were unrelated. Under all water regimes genotypic differences were marginal for both dry matter and physiological parameters, indicating that differences in stress-sensitivity did not exist. Δ was proven to be a sensitive indicator for water availability during the growing period. However, similar to other parameters relevant for drought tolerance it requires investigations in broader genetic material of sugar beet to detect genotypic differences.

Section IV "Solute accumulation as a cause for quality losses in sugar beet submitted to continuous and temporary drought stress" focuses on the effects of drought on the chemical composition of the sugar beet taproot. Increasing dry matter concentration with decreasing water supply could in part be attributed to an increase in the concentration of cell wall components. The major solutes in the taproot were sucrose, potassium, amino N (the sum of amino acids) and betaine. Sucrose concentration decreased considerably under drought, indicating limited availability of assimilates. In

contrast, all further solutes increased in concentration with increasing severity of stress. However, the response of individual solutes varied largely. Changes in amino N and nitrate were most pronounced and reflect probably accumulation of non-utilized metabolites under limited growth. The drought-induced accumulation of taproot solutes implicates a considerable decrease in the technical quality of the beet. It was only in part reversible by re-watering. Genotypic variability for solute accumulation under water deficiency was observed but was not linked to drought tolerance.

Conclusions

Our investigations show that in dependence on its severity water shortage is responsible for significant reductions in sugar beet leaf yield. Together with limitations in stomatal conductance and hence carbon dioxide assimilation this resulted in markedly reduced growth of the taproot as well. Reductions in leaf yield, however, were larger than in taproot yield resulting in an increased taproot-to-leaf-ratio under drought. Significant amounts of solutes are accumulated in the taproot leading to losses in technical quality of the beet. Amino acids and nitrate are quantitatively of highest importance, whereas changes in potassium, sodium and betaine are less pronounced.

Genotypic differences in field grown sugar beet emerge very early in the vegetation period. Differences in taproot and leaf yield as well as in parameters of technical quality were established already at the end of June. From this time on there seems to be little potential for differing response patterns even in genetically heterogenous material of sugar beet. Different sugar beet genotypes responded identically to changing environmental conditions during the vegetation period as there were no interactions between genotype and harvest date. For almost all parameters studied, interactions between genotype and irrigation did not occur either, indicating that water supply as a single determinant of the environment affected all genotypes in the same way. Also fundamental physiological mechanisms of yield formation were affected in different genotypes to the same degree. Genotypic differences in drought-induced solute accumulation appeared only under controlled conditions in the greenhouse and did not imply differences in stress sensitivity.

It is concluded that at the time there is no possibility to improve sugar beet productivity in drought-prone areas by the use of tolerant varieties. Further

investigations have to reveal to which extent there is genotypic variability for drought tolerance in a broader genetic base of sugar beet and which are the mechanisms involved.