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Impact of water supply on photosynthesis, water use and carbon isotope discrimination of sugar beet genotypes

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Abstract

Improvements in drought tolerance of crop plants require research focused on physiological processes. In 2002 and 2003 pot experiments with sugar beet were conducted in a greenhouse. Two (2002) or three (2003) different genotypes were subjected to three watering regimes (100, 50 and 20% of water holding capacity). Gas exchange, chlorophyll fluorescence and water-use efficiency (WUE) as parameters of possible relevance for drought stress tolerance in sugar beet were investigated. It was studied whether ^{13}C discrimination (Δ) is suitable as an indirect measure for WUE of sugar beet.

DM yield, photosynthesis rate, transpiration rate and stomatal conductance decreased with increasing severity of drought stress. In contrast, internal CO_2 partial pressure remained relatively stable and effective quantum yield of photosynthesis was reduced only under severe drought, which points at non-stomatal inhibition of photosynthesis. Different sugar beet genotypes showed significant differences in DM yield, but interactions between genotype and water supply did not occur, indicating that genotypic differences in drought tolerance did not exist. In accordance with that, drought-sensitivity of gas exchange and chlorophyll fluorescence was the same in different genotypes. Δ was higher in the leaves than in the taproot. Reductions in Δ in drought-stressed plants corresponded to about 24% higher WUE. Differentiating between plant organs, only leaf Δ was negatively correlated with WUE_L whereas taproot Δ and WUE_T were unrelated. Δ was therefore proven to be a sensitive indicator for water availability during the growing period. However, similar as other parameters relevant for drought stress tolerance it requires investigations in broader genetic material of sugar beet to detect genotypic differences.

Keywords: Sugar beet; Drought stress; Water-use efficiency; Carbon isotope discrimination; Chlorophyll fluorescence; Gas exchange

1. Introduction

Low water availability is one of the major causes for crop yield reductions affecting the majority of the arable land around the world. As water resources for agronomic uses become more limiting, the development of drought-tolerant cultivars gains in importance (Bruce et al., 2002; Ober, 2001). In commercial varieties of sugar beet considerable variability for drought tolerance in terms of yield and quality has not been found so far (van der Beek and Houtman, 1993; Bloch and Hoffmann, 2005). Generally, a number of mechanisms can contribute to an improved drought tolerance of crop plants, including morphological characteristics like deep rooting or metabolic regulatory mechanisms like osmotic adjustment. Also the use of physiological traits is very relevant for crop improvement in dry environments. However, little research is done on direct effects of stress factors on physiological processes affecting dry matter production. The investigation of mechanisms of drought tolerance in sugar beet therefore requires research focused on physiological processes such as photosynthesis, assimilation and degradation and translocation mechanisms (van der Beek and Houtman, 1993).

When plants encounter water deficit, there is a decline in photosynthesis. This can be due to a reduction in light interception as leaf expansion is reduced or as leaf senescence is accelerated. But it can also be attributed to reductions in C fixation per unit leaf area as stomata close or as photo-oxidation damages the photosynthetic mechanism (Bruce et al., 2002). Much of the reduction in CO_2 assimilation under water deficit is due to stomatal closure (Arnau et al., 1997). In plants, higher stomatal conductance increases CO_2 diffusion into the leaf thereby favouring higher net photosynthetic rates which could in turn

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Abbreviations: DM, dry matter; WUE, water-use efficiency; WUEi, instantaneous WUE (or leaf transpiration efficiency); WUE_L, leaf DM-based WUE; WUE_T, taproot DM-based WUE; Δ, carbon isotope discrimination; PAR, photosynthetic active radiation; WHC, water holding capacity

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increase biomass production and thereby crop yield. Genotypic differences in stomatal conductance can be linked to variability for drought resistance (Blum et al., 1989); e.g. accessions of *Oryza* with higher stomatal conductance under stress were shown to maintain leaf elongation better than other genotypes (Liu et al., 2004). In contrast, in barley (Arnau et al., 1997) or okra (Ashraf et al., 2002) significant genotypic differences for stomatal conductance were not found. In sugar beet, data on the drought-sensitivity of gas exchange of different genotypes are lacking.

Part of the effect of drought on photosynthesis can also be attributed to direct inhibitory effects of water deficiency on CO_2 fixation (Sharkey and Seemann, 1989). As photosystem II appears to be particularly sensitive to a number of stress factors, chlorophyll fluorescence is used as a tool in revealing stress response mechanisms and in quantifying these responses (Bolhár-Nordenkampf and Öquist, 1993). An increase in fluorescence emission and therefore a decrease in effective quantum yield characterizes a decrease of the overall photosynthetic capability of the plant. Chlorophyll fluorescence has been used by plant breeders to quantify rapidly the response of different varieties or lines to certain stresses. Ranalli et al. (1997) have shown the potential use of chlorophyll fluorescence as a tool for screening drought tolerance of potato germplasm. Also in sugar beet chlorophyll fluorescence has been used to assess the response of different genotypes to drought stress (Clarke et al., 1993; Mohammadian et al., 2003). However, results have been obtained in field studies only where the impact of drought stress cannot be separated from simultaneous effects of other stress factors.

Higher water-use efficiency (WUE) is mentioned as a strategy to improve crop performance under water-limited conditions (Araus et al., 2002). WUE usually is defined as the total dry matter produced by plants per unit of water used (Boyer, 1996). Instead of total dry matter, WUE can also refer to the economically valuable part of the crop only or to the water use of a single leaf. A relationship between WUE and carbon isotope discrimination was first described by Farquhar and Richards (1984). During uptake of CO_2 from the atmosphere plants discriminate against the heavier carbon isotope ^{13}C. The discrimination of ^{13}C (Δ) is calculated as the $^{13}C/^{12}C$ ratio in plant material relative to the value of the same ratio in the air on which plants feed. It is linked to the plants' capability to reduce the CO_2 partial pressure in the intercellular spaces. The smaller the CO_2 partial pressure inside the plant in comparison to the partial pressure in the atmosphere, the less the plants discriminate between the two isotopes (Δ more positive) and the greater is WUE (Ehlers and Goss, 2003). The correlation between WUE and Δ has been extensively studied in several field crops including common bean (*Phaseolus vulgaris* L.) (Ehleringer, 1990), wheat (Farquhar and Richards, 1984; Condon et al., 1990), peanut (*Arachis hypogea* L.) (Wright et al., 1994), barley (*Hordeum vulgare* L.) (Acevedo, 1993) and cowpea (*Vigna unguiculata* [L.] Walp.) (Ismail et al., 1994). These studies suggest that genetic variation in Δ may be sufficient to be useful as a selection tool for improved water-use efficiency. In a study comparing 20 commercial sugar beet varieties, Δ in the leaves was only marginally affected by variety (Tsialtas and Karadimos, 2003). However, data on the correlation between WUE and Δ in sugar beet are lacking.

The aim of this study was to determine gas exchange, chlorophyll fluorescence and water-use efficiency as parameters of possible relevance for the detection of drought stress tolerance in sugar beet. Genotypic differences in drought stress tolerance are expected to be related to differences in these parameters. It was studied whether Δ is suitable as an indirect measure for WUE of sugar beet.

2. Materials and methods

2.1. Plant material

Pot trials were conducted in 2002 and 2003 in the greenhouse. The vegetation period was from May to November 2002 and from March to August 2003. Pelleted, pregerminated seeds of *Beta vulgaris* L. were sown in 30 L plastic pots (40 cm in height and 32 cm in diameter) containing 42 kg of medium sand. In order to obtain uniform plant establishment, seedlings were thinned from 12 to 2 per pot after emergence. The substrate was additionally covered with 1 kg of coarse quartz sand to prevent evaporation. Plants received optimal nutrient supply according to Winner and Bürcky (1977), split into four applications of a nutrient solution. Each pot was supplied with a total of 5315 mg N, 2610 mg P, 6884 mg K, 2000 mg S, 590 mg Na, 1820 mg Cl, 7985 mg Ca, 1750 mg Mg, 100 mg Fe and microelements.

2.2. Water regimes

Water supply was varied in three levels, according to 100 (control), 50 and 20% of water holding capacity (WHC). Water content at maximum water holding capacity was determined as the amount of water retained by representative samples of the substrate at pF 1.8, determined gravimetrically by subsequent drying of the samples at 105 °C for 24 h. Water regimes were implemented 6 (2003: 9) weeks after sowing. Adjustment of the intended water contents was accomplished on a weight basis every second day.

2.3. Genotype selection

Two (2002) or three (2003) genotypes of *Beta vulgaris* L. were grown. The selected genotypes were expected to represent a wide range of drought tolerance as they comprised the commercial German variety Cynthia (A), a variety which has been successful over years in the Italian sugar beet cultivation and is regarded as drought tolerant (Dorothea, B) and the hybrid HI0097 which is putative drought susceptible due to reductions in the root system (C).

2.4. Harvest

Plants were harvested 24 and 20 weeks after sowing in 2002 and 2003, respectively. Harvest dates corresponded to 34- (2002) and 28-leaf stage (2003) for the control plants. Drought-stressed plants had about 6 (50% of WHC) or 10 (20% of WHC) leaves less. The number of replications per treatment amounted to 6 in 2002 and 5 in 2003. The pots were arranged completely randomized.

At harvest, plants were separated into taproot and leaf (including crowns, i.e. the uppermost part of the taproot where leaves emerge, morphologically being part of the shoot). Taproots were washed, taproot and leaf fresh mass were determined and mashed samples of both fractions were oven-dried at 105 °C for 24 h in order to determine the dry matter (DM) content.

2.5. Measurements

CO_2/H_2O gas exchange and radiation intensity were measured using the portable porometer CIRAS S/N 110 (Combined Infrared Gas Analysis System, PP Systems, GB). Net photosynthesis rate, stomatal conductance, internal CO_2 partial pressure and transpiration rate were determined at the tip of recently fully-expanded leaves avoiding major veins. The leaf cuvette (PLC N, PP Systems, GB) covered a leaf area of $4.5\,\mathrm{cm}^2$. The reference air stream had a flow rate of $5\,\mathrm{cm}^3\,\mathrm{s}^{-1}$ at 20 °C and 1 bar air pressure. Its CO_2 concentration and water content were set to 350 ppm and 99% of the ambient air at the time of the measurement. The photosynthetic active radiation (PAR) was determined by a sensor on the leaf cuvette. Measurements were made on sunny days with a low cloud cover.

Leaf chlorophyll fluorescence was measured using the photosynthesis yield analyzer MINI-PAM (Portable Chlorophyll Fluorometer, Walz, Effeltrich, Germany). The used fluorescence parameter was $\Delta F/F_m'$ (effective quantum yield of photosynthesis), which is calculated as:

$$(F_m' - F_t)/F_m'$$

with F_m' being the chlorophyll fluorescence signal at its intermediate maximum and F_t being the steady state signal (Schreiber and Bilger, 1987).

^{13}C discrimination (Δ) was determined for leaf and taproot material in 2002. Carbon isotopes were analyzed using an isotope mass spectrometer Finnigan MAT (Bremen, Germany) DELTA^{plus} coupled via Conflo-III interface to an elemental analyzer NC 2500 (CE Instruments Rodano, Milano, Italy). The measuring principle was described in detail by Werner et al. (1999). Carbon isotope effects are calculated as:

$$\delta^{13}C = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 10^3$$

with R_{sample} and R_{standard} being the $^{13}C/^{12}C$ ratios of the sample and the standard Pee Dee Belemnite, respectively. Carbon isotope discrimination was calculated as:

$$\Delta\,(‰) = (\delta_{\text{air}} - \delta_{\text{plant}})/(1 + \delta_{\text{plant}} \times 1000)$$

where $\delta^{13}C$ of air CO_2 is $-8‰$.

2.6. Water-use efficiency

Water-use efficiency was calculated in two different ways: (1) from gas exchange measurement data dividing instantaneous net assimilation by instantaneous transpiration rate (WUEi) and (2) by integrating over the vegetation period dividing accumulated dry matter by cumulative water use (WUE). The latter was calculated for total DM and for leaf and taproot DM separately.

2.7. Statistics

An ANOVA was carried out with the program SAS version 8.1 (SAS Institute Inc., Cary, NC, USA) using the GLM procedure. Ryan–Einot–Gabriel–Welsch multiple range test (REGWQ-test) was used to detect significant differences ($\alpha = 0.05$) among means. The REGWQ-test is a sequential (stepwise) multiple comparison procedure and there is no uniform LSD for all comparisons but the critical difference depends on the number of means to be compared. The relationship between WUE and Δ was described with a linear regression function.

3. Results

Drought stress (50 or 20% WHC) imposed for a period of 18 (2002) or 11 (2003) weeks on 6- (2002) or 9- (2003) week-old sugar beet plants led to significant reductions in taproot and leaf dry weight (Table 1). Genotype A had both higher leaf and

Table 1
Taproot and leaf dry weight of sugar beet as affected by genotype (G) and water supply (W)

	Water supply[a]	Genotype			Genotype		
		Taproot dry weight (g per plant)			Leaf dry weight (g per plant)		
		A	B	C	A	B	C
2002	100	175.5	151.9		74.7	70.3	
	50	95.0	76.6		49.4	47.9	
	20	22.9	15.4		22.2	19.8	
			W^{***}; G^{**}; W × G n.s.			W^{***}; G n.s.; W × G n.s.	
2003	100	125.7	121.0	110.9	58.0	56.5	44.7
	50	69.6	72.5	64.6	33.9	33.3	29.3
	20	10.1	9.1	8.6	12.3	13.2	13.0
			W^{***}; G^{**}; W × G n.s.			W^{***}; G^{**}; W × G^{*}	

Treatments started at 6 (2002) or 9 (2003) weeks after sowing and lasted 18 (2002) or 11 (2003) weeks. Significant differences are indicated with *, ** or *** for $\alpha < 0.05$, 0.01 or 0.001, n.s. = not significant.

[a] % of water holding capacity.

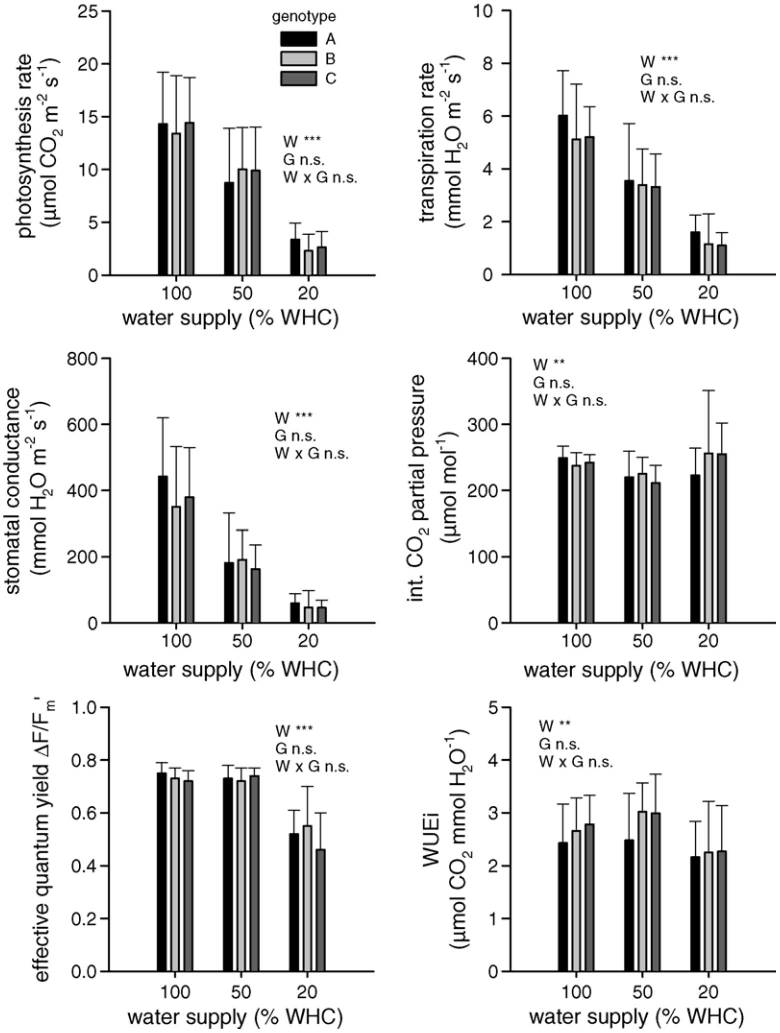

Fig. 1. Gas exchange and chlorophyll fluorescence parameters of sugar beet as affected by genotype (G) and water supply (W) (WHC, water holding capacity). Pot experiment 2003, means ± S.D. from measurements on July 31st, August 1st and 5th. Significant differences are indicated with ** or *** for $\alpha < 0.01$ or 0.001, n.s. = not significant.

taproot dry matter than genotype B, and genotype C had the lowest dry matter production. Reductions in taproot and leaf DM due to drought stress were similar in all genotypes. A significant interaction between genotype and water supply occurred only for leaf dry weight in 2003.

Gas exchange data are presented from the 2003 experiment, when three genotypes had been compared. Results from the comparison of two genotypes in 2002 were similar. Photosynthesis rate, transpiration rate and stomatal conductance of all sugar beet genotypes decreased with increasing water deficit (Fig. 1). Internal CO_2 partial pressure was slightly decreased under moderate drought (50% WHC), whereas instantaneous WUE (WUEi) and effective quantum yield of photosynthesis were decreased only under severe drought (20% WHC). The effect of the genotype and the interaction between genotype and water supply were non-significant for all parameters measured. As a mean of all genotypes, leaf DM concentration amounted to 13.5, 18.0 and 26.5% under 100, 50 and 20% of water holding capacity, respectively, at the time of the gas exchange measurements (data not shown).

Data on water-use efficiency (WUE) calculated as integrated values of the entire vegetation period are presented from the 2002 experiment only, when ^{13}C discrimination was also determined. When based on total plant dry matter, WUE increased with increasing severity of drought stress (Fig. 2). While leaf-based WUE was higher for stressed plants as well, taproot-based WUE was not distinctly affected by water supply. In tendency, genotype A obtained higher WUE than genotype B in all treatments.

Δ was higher (more negative values) in leaf than in taproot dry matter (Fig. 3) and decreased with decreasing water supply. Genotypic differences for Δ were not significant. There was no relationship between taproot Δ and WUE_T, but leaf Δ was negatively correlated with WUE_L (Fig. 4). Here, the regression was almost identical for both genotypes.

4. Discussion

In these experiments, different moisture contents of the substrate were chosen to simulate sufficient water supply as well

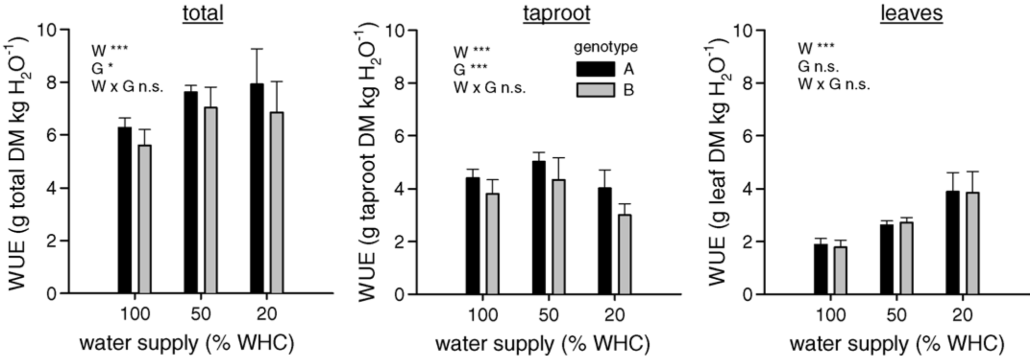

Fig. 2. Water-use efficiency (WUE) of sugar beet as affected by genotype (G) and water supply (W) (WHC, water holding capacity). Treatments started at 6 weeks after sowing and lasted 18 weeks. Values are based on total DM (left), taproot DM (middle) and leaf DM (right). Pot experiment 2002, means ± S.D. Significant differences are indicated with * or *** for $\alpha < 0.05$ or 0.001, n.s. = not significant.

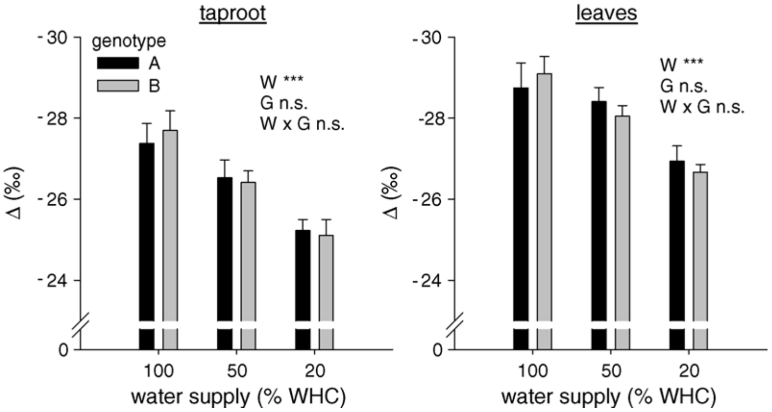

Fig. 3. ^{13}C discrimination (Δ) in taproot and leaves of sugar beet as affected by genotype (G) and water supply (W) (WHC, water holding capacity). Treatments started at 6 weeks after sowing and lasted 18 weeks. Pot experiment 2002. Vertical bars indicate ±1 S.D. Significant differences are indicated with *** for $\alpha < 0.001$, n.s. = not significant.

as stress conditions of different severity. It was not possible to maintain the moisture contents constantly at the target values by watering every second day. The plants dried the soil as time progressed and there was probably also a gradient in water content from the top of the pot to the bottom. However, these conditions represented distinctly different water availability, and a certain spatial and temporal variation in water content appeared probably in all treatments likewise. Furthermore, no attempt was made to quantitatively relate the changes in growth or physiological parameters to specific changes in soil water potential.

4.1. Plant growth and photosynthesis

Drought stress significantly reduced taproot and leaf dry matter production of the plant. These reductions in dry matter were associated with changes in various parameters of photosynthesis. Gas exchange was strongly affected under drought stress. The photosynthesis rate continuously decreased with increasing severity of stress. This decrease could be explained by reductions in stomatal conductance, which reduced CO_2 diffusion. However, internal CO_2 partial pressure remained relatively stable,

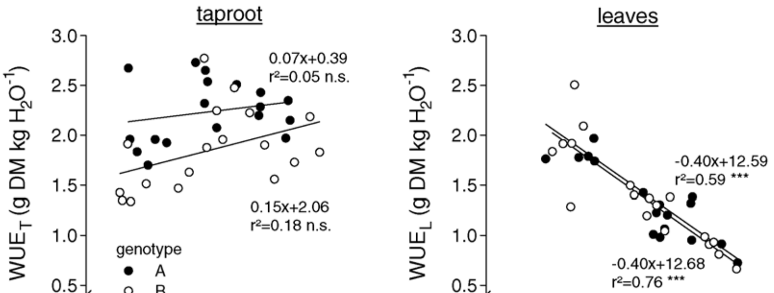

Fig. 4. Relationship between water-use efficiency (WUE) and ^{13}C discrimination (Δ) in taproot and leaves of two sugar beet genotypes. Pot experiment 2002. Significant differences are indicated with *** for $\alpha < 0.001$, n.s. = not significant.

particularly under severe drought it was similar to that observed in well-watered plants. Thus, reduced stomatal conductance is not supposed to be the major cause of reduced photosynthesis, and the effect of severe drought stress on photosynthesis has to be attributed also to non-stomatal effects (Kirkham, 1990). Generally, the severity of the stress appears to be important in determining whether non-stomatal factors affect photosynthesis, as inhibition of mesophyll activity (non-stomatal inhibition of photosynthesis) in addition to stomatal closure occurs only during severe or prolonged stress.

In accordance with that, effective quantum yield of photosynthesis was reduced only under severe drought. In sugar beet, damage of the photosynthetic pathway under water deficit was also reported by Clarke et al. (1993) and Mohammadian et al. (2003). Clover et al. (1999), in contrast, did not observe an effect of drought on chlorophyll fluorescence of sugar beet leaves and attributed findings of damage of the photosynthetic pathway to a premature senescence of drought stressed leaves. In the present experiment, however, leaves chosen for chlorophyll fluorescence measurements were relatively young and of a uniform developmental stage in all treatments, so that an effect of premature senescence is rather unlikely. Further experiments have to be conducted to examine the influence of drought sequentially for young and older single leaves under conditions of different stress severity.

Genotypic differences for parameters of photosynthesis were not detected. Therefore, variation in yield performance could be explained rather by differences in leaf DM, which was higher in genotypes with higher taproot dry weights. However, yield reductions under drought were the same in all genotypes, which is in accordance with the lack of genotypic differences for sensitivity of the photosynthetic apparatus.

4.2. Water-use efficiency

Although no genotypic differences in parameters of photosynthesis under stress were found, genotypes may differ in water-use efficiency. Generally, dry matter production and water use of crop stands are closely related and the relationship between cumulative water use and yield, characterized by the water-use efficiency (WUE), is to a large extent independent of the level of water supply and water use (Ehlers and Goss, 2003). However, in the present study the relationship between water use and yield was modified by water supply. As a mean of both genotypes in the 2002 experiment, WUE amounted to 6.0, 7.3 and 7.4 g total DM per L H_2O for control, moderate and severe drought, respectively, which is in a similar range as values reported for sugar beet by Clover et al. (2001), Dunham (1989) or Roth et al. (1988). Increased WUE values under drought have been described by Brown et al. (1987) and Clover et al. (2001) as well. The higher efficiency of water use under stress is due to the fact that drought-stressed plants wilt far more than unstressed plants and wilting invariably occurs in times when the saturation deficit of the atmosphere is large. Therefore, the plant assimilates only in times when the saturation deficit is small and hence loses less water for every carbon molecule fixed (Clover et al., 2001). However, the increase in the efficiency of water use under drought stress occurs at the expense of absolute yield performance. Differences in WUE may therefore need to be combined with other crop traits to be of practical value for crop improvement in dry environments.

Genotype A obtained higher DM in all treatments and hence used the water more efficiently than genotype B. However, the lack of interaction between genotype and water supply for WUE suggests that genotypes, which are most productive under well-watered conditions will also be superior in dry environments.

WUEi values, obtained by short-term gas exchange measurements, were not clearly affected by water supply and did therefore not appropriately describe the effect, which appeared when integrated values of the entire vegetation period were used. Often the relationship between short-term gas exchange efficiency and the actual water-use efficiency for the whole growing season is poor, because there is a number of factors affecting dry matter accumulation but not gas exchange (Boyer, 1996). For example, the biomass production of a plant is not only determined by photosynthesis but also by respiratory losses at night. It is altered by temperature and the molecular composition of the dry matter. Gas exchange determination for short times during the day does not detect these additional factors. Therefore, although rapid and convenient, gas exchange measurements are not suitable to reliably assess differences in WUE.

4.3. ^{13}C discrimination

^{13}C discrimination (Δ) was higher in sugar beet leaves than in the taproot. Differences in Δ between plant organs have been reported for various species (e.g. peanut, Hubick and Farquhar, 1989; canola, Matus et al., 1995) but reasons for these findings have not been clearly established. According to Zhao et al. (2004) products of secondary metabolism, such as roots and grain, usually have lower Δ values than primary photosynthetic products, such as leaves. Brugnoli and Farquhar (2000) suggested that possible reasons for explaining these differences include: (1) fractionation during export, phloem loading and unloading and transport of carbohydrate from photosynthetic to storage organs and (2) different chemical composition of different organs. For example, a higher content of lipid and lignin may lead to a relative depletion in ^{13}C, while higher cellulose contents lead to a relative enrichment. Farquhar and Richards (1984) found lower Δ in wheat grain as compared to leaf material, which was attributed partly to the higher nitrogen content of the grain. The formation of carbon skeletons for some amino acids involves phosphoenolpyruvate carboxylation, which discriminates in favour of ^{13}C. However, this possibility does not match the present results as Δ was lower in the sugar beet taproot although its amino nitrogen content is about two-fold lower compared to the leaf and crown fraction (Mäck and Hoffmann, 2004).

Δ was lower in drought-stressed plants than in plants supplied sufficiently with water. Reductions in Δ under drought have been reported for many plant species, e.g. for wheat (Sayre et al., 1995), white clover (Hogh Jensen and Schjoerring, 1997), soybean (Kao and Tsai, 1998), peanut (Craufurd et al., 1999) and rice (Pinheiro et al., 2000). For sugar beet leaf, Tsialtas and Karadimos (2003) found lower Δ values when plants were grown in a drought-prone area compared to those from a less arid climate. In our experiment, the relationship between Δ and water availability was proven for both leaf and taproot material.

A negative correlation between Δ and WUE was first described by Farquhar and Richards (1984) for wheat genotypes. In the present study genotypes did not significantly differ in Δ values. However, variation in Δ and in WUE was provoked by the different water regimes. A negative correlation occurred only between leaf Δ and $\mathrm{WUE_L}$, whereas for the taproot there was no relationship between Δ and WUE as $\mathrm{WUE_T}$ at final harvest was not distinctly affected by water supply. Zhao et al. (2004) similarly reported on a weakening of the correlation between WUE and Δ in upland rice through the inclusion of root dry matter in addition to aboveground dry matter.

In a first attempt to use Δ in sugar beet research, Tsialtas and Karadimos (2003) did not find a relation between leaf Δ and sugar beet fresh root yield. However, under water deficit the productivity of a crop is determined also by its water-use efficiency for which Δ seems to be a reliable predictive criterion. Its practical application in sugar beet improvement under drought stress requires genetic variability. However, this is likely to be found only within a broader genetic base of the section *Beta*.

5. Conclusion

Physiological characteristics, which show a distinct response to drought stress can be of importance for genotypic differences in the performance under stress. In the present experiment differences between genotypes in various stress-sensitive physiological characteristics were marginal which was in accordance with the lack of interactions between water supply and genotype for dry matter production and water-use efficiency. However, in consideration of the expected heterogeneity of the genotypes under study the low genotypic variability was surprising. The investigation of genetically broader material of sugar beet would possibly help detect differences in yield response as well as in physiological traits relevant for selection for drought tolerance.

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