Growth and dry matter partitioning in sugar beet plants (*Beta vulgaris* L.) under moderate drought

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ABSTRACT

Growth response of sugar beet plants to drought stress applied at different growth stages has been investigated. Cessation of watering imposed moderate water stress and resulted in the reduction of the relative water content of young and old leaves maximally by 6%. However, water content in taproot was more drastically decreased than in the shoot. Water withholding reduced dry matter accumulation and leaf assimilatory expansion when imposed at successive growth stages, especially in the case of earlier stress application. Substantial change in distribution pattern was observed when stress affected foliar development, more than 80% of dry matter was accumulated in the taproots. Water shortage negatively influenced both taproot and sugar yield by 16–52%, depending on the stress timing in the season. Drought stress did not change the sucrose concentration but when occurred in foliar and early stage of root development, decreased the contents of important non-sugar compounds like potassium and α-amino-N solutes in the final yield. Overall, data concerning the different water status in particular organs implies that a hydrodynamic equilibrium does not exist within the sugar beet plant as a response to water stress. Drought imposed on the earlier stage, most drastically influenced plant growth and final yield. When water stress occurs at the end of crop cycle, sugar beet plants had a higher ability to recovery their growth.

Keywords: *Beta vulgaris* L.; drought; dry matter partitioning; growth; leaf area; water content; yield quantity and quality

Drought stress has become the major limitation factor on plant yield at global scale (Starck et al. 1995, Yordanov et al. 2000). It is due to the current environmental changes not only in dry areas but also in temperate ones. Under Polish climatic conditions, intermittent water deficiency is one of the dominant factors, which limit sugar beet plant productivity (Pidgeon et al. 2000). Plant response to water deficit dependent on the length and severity of water lost and also on the species or genotype, as well as on the age and stage of its development. Drought as a multidimensional stress affected plants at various: subcellular compartment, cell, organs and whole plant levels of their organisation. The plant response to drought at the crop level is complex because it reflects the integration of stress effects at all underlying levels of organisations over space and time (Blum 1996).

When soil water is gradually depleted, a number of plant functions are inhibited but leaf growth is one of the first to diminish (Hsiao 2000). It is clear that both, cell production and cell expansion can be negatively influenced by mild water deficit, but much more attention has been given to the modification of cell expansion, presumably because a role of turgor variation which is easier to understand in this context. Nevertheless, the growth of shoot is often restricted as soil dries, even when shoot turgor is completely maintained (Kramer and Boyer 1995). In an early study, Milford and Lawlor (1976) showed that even a small changes in sugar beet leaf water potential of 0.2–0.3 MPa drastically decrease its growth rates; leaf expansion stops altogether when the leaves start wilting at round – 1.5 MPa but growth is impaired long before wilting is observed. They also indicated the different wilting patterns of young and mature sugar beet leaves. Mature leaves loss turgor when the plant is severely water-stressed in spite of low stomata conductance and reduction of transpiration but young leaves usually remain upright although their stomata maintain open. In dry soil, root growth is much less depressed than shoot growth and there is typically a decrease in the shoot to root dry weight ratio in response to drought stress (Hsiao 2000). This was also observed in putative drought tolerant, sugar beet genotype on account of considerable reduction in shoot growth which was compensated for by a large increase in fibrous root development (Shaw et al. 2002). At the same time drought intolerant genotype showed a similar reduction in both shoot and taproot growth, but there was less change in fibrous root development. Abdollahian-Noghabi and Froud-Williams (1998)

also noted a drastic reduction in the leaf area and a smaller decrease in the taproot growth of sugar beet when subjected to drought stress. Overall, there is a sharp contrast between the root and the shoot in their response to water deficit. It could be explained by different rate of osmotic adjustment of shoot and root cells (Hsiao 2000) or various loosening ability of leaf cell walls from roots cell walls. Loosening ability of the growing cell wall could be affected by auxins and also by ABA. Under water stress, the concentration of endogenous ABA increases in both leaves and roots and more ABA is transported from root to the shoot (Davies and Zhang 1991). Simultaneously, convincing evidence was obtained indicating that ABA maintains root growth while inhibiting shoot growth in soybean (Creelman et al. 1990) and in maize (Saab et al. 1990) at low water potential conditions. Thus, ABA may act as a signal for the initiation of regulatory processes involved in the differential long-term growth responses of root and shoot to water deficit (Davies et al. 1994).

Sugar beet plants possess an effective mechanism for osmotic adjustment (Clarke et al. 1993). Unfortunately, α-amino-N compounds, glycine betaine and proline (Gzik 1996, Rover and Buttner 1999), along with sodium and potassium which accumulate in sugar beet taproot following water stress, are principal impurities that reduce sugar beet quality for processing by inhibiting crystallisation during processing (Clarke et al. 1993).

Thus, drought negatively affects quantity and quality of sugar beet yield. Since there is need to achieve better understanding of its coping with this stress, our experiments were conducted to investigate sugar beet plant growth response to drought stress imposed in different vegetative growth stages.

MATERIAL AND METHODS

Sugar beet seeds cv. Janus, were generously supplied by Kutnowska Sugar Beet Breeding Company (KHBC Ltd., Poland). This cultivar has big root yield of high technological quality and of high sugar content. Plants were grown in plastic tunnels (25 m length and 5 m wide) in moderate soil with pH maintenance on about 6.0–6.5. Plant density was finally cared for 10 plants per m^2. Plants were grown, according to standard fertilisers (330 kg/ha pure nutrients of NPK) and pesticides.

The plants had different water supplies: control (automatic irrigation to obtain 60% of the water field capacity) and drought (automatic irrigation to obtain 30–35% of the water field capacity). The water shortage was imposed at 27 days at timed intervals at different stages of plant development: 36 days after emergence (DAE) at the stage of foliar development, 4–5 leaf (D1) or at 63 DAE – at the beginning of root development (D2) and at 113 DAE – with the intensive accumulation in root (D3).

Fresh and dry matter of particular plant organs (blades, petioles, and taproots) was determined at 36, 63, 92, 141 and 161 DAE (harvest time) and water content of sugar beet organs (%) was calculated. Just after cessation of drought, relative water content (RWC) in leaves of different growth stages (young, mature and senescing) was measured using the methods of Weatherly (1949). Leaf Area Index (LAI) and was recorded a few times during plant growth using LAI-2000 (LICOR-USA). Relative

Table 1. Effect of 27 days drought stress on the water content (%) of individual organs and on the relative water content (RWC, %) of leaves in sugar beet plants

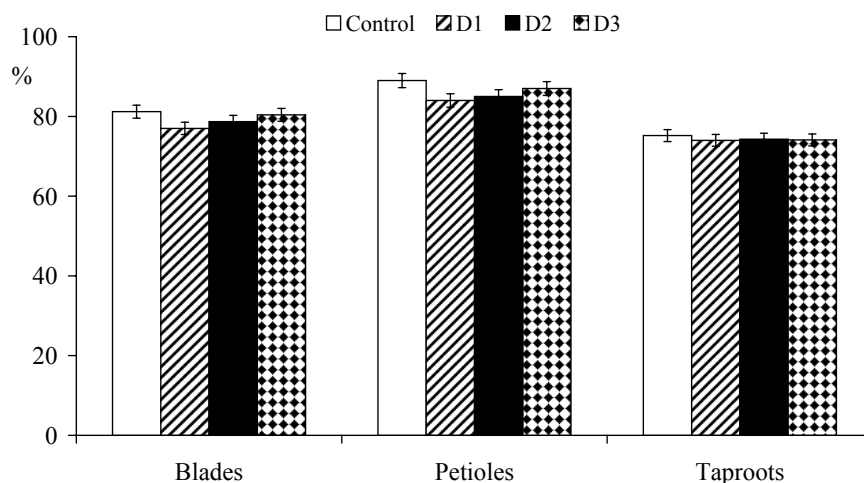| DAE		63		92		141	
		control	D1	control	D2	control	D3
Water content of particular organs (%)							
Organs	blades	90.3	**86.6**	89.3	**86.2**	83.4	**82.0**
	petioles	91.2	**88.0**	90.0	**86.4**	90.0	**87.7**
	tap roots	82.4	**77.0**	79.2	**74.7**	76.5	**74.9**
	LSD	0.77		1.66		1.07	
RWC (%)							
Leaves	old	92.3	**87.9**	95.3	**91.1**	97.5	96.3
	mature	89.8	90.0	91.3	90.6	97.4	96.7
	young	85.0	**81.6**	87.4	86.3	93.1	**86.9**
	LSD	2.8		3.7		2.7	

Figure 1. Effect of 27 days of drought on the water content of individual organs of sugar beet plants examined after different time of recovery (161 DAE)

growth rates (RGR) for individual plant organs were also calculated.

The quality of sugar beet yield: concentration of K^+, Na^+, α-amino-N compounds in taproots was examined using standard Venema line in co-operation with KHBC Ltd., Poland. Inorganic phosphorus level was measured using the methods of Ames (1966).

Data from these experiments were analysed by analysis of variance using t-Student test for *LSD* calculation and are described as significant at the $P < 0.05$ level.

RESULTS

Water shortage negatively affected water content of sugar beet blades and petioles and taproots in the cases of all drought treatments. However, the shoot contained more water than the root when well watered and drought stressed (Table 1). As a consequence of withholding water, its content in root was more drastically reduced than in the shoot. Nevertheless, drought imposed at earliest stage of plant development reduced plant water content more severe than other periods of stress applied. Relative water content (RWC) of leaves, measured just after cessation of drought, was differently affected by water shortage depending of the stage of their development and time of stress treatment (Table 1). RWC of young leaves was decreased by 4% in effect of the first and third drought treatments but in old leaves relative water content was reduced in the case of first and second time of stress applied. Simultaneously, RWC of mature leaves was unaffected by water shortage independently of time of stress treatment. Water content of shoot, measured at harvest time, was still lower in all drought-stressed plants then in well-watered when water status of taproot fully recovered (Figure 1).

It was found that, all drought treatments at successive growth stages reduced dry matter of the whole plants during application of a water shortage (Figure 2A), especially in the case of D1 and D2. The recovery of plants that submitted to temporary drought was possible only if the stress was imposed at a very late growth stage, whereas at 4–5 leaves or at root expansion stages it has never succeeded. Water shortage imposed at early stages dramatically hampered leaf assimilatory expansion (Figure 2B). Neither after drought at stage D1 nor after that at D2 were plants able to reach an optimum LAI. Optimum LAI in our experiment reached by the control plants was nearly 4.5.

Substantial change in distribution pattern as affected by water shortage was strongly caused by stress imposing during early growth of the assimilatory surface, at the stage of 4–5 leaves (Figure 2C). It resulted in suddenly reoriented dry matter distribution towards the roots (more than 80% of dry matter accumulated in the taproots), followed by intensive leaf regrowth. It was also found in the case of a water deficit applied in the later stage of plant development (D3) but in a much less extent. During the different times of recovery, a fraction of assimilate partitioned to storage was higher in stressed plants than in comparison with the well watered plants.

Severe reduction in relative growth rate (RGR) of the shoot (Figure 3A, B) was denoted when drought affected the whole examined stage of plant development, while substantial increase of RGR of leaves just after cessation of drought imposed at D3 stage enabled stressed plants to recover. In contrast, RGR of taproots was unaffected by water shortage independently from time of stress treatment. Thus, in the result of different effects of drought on shoot and root growth and changes in dry matter partitioning, water shortage imposed at the whole stage of plant development increased root to shoot ratio (Table 2).
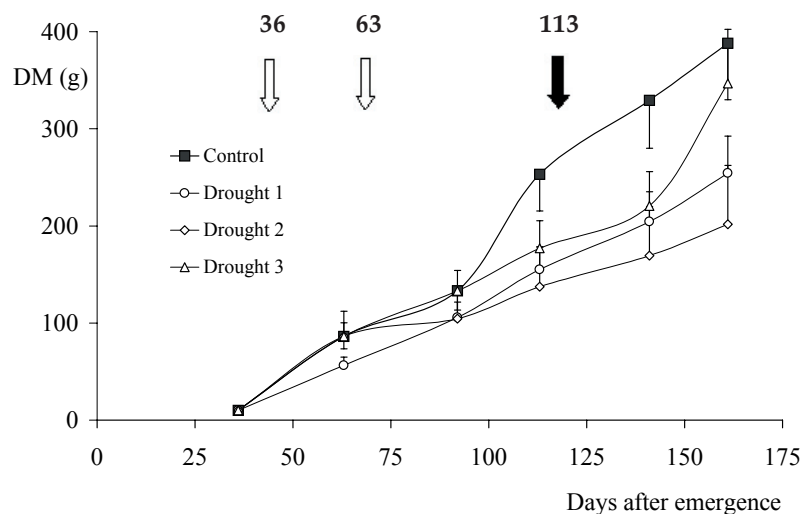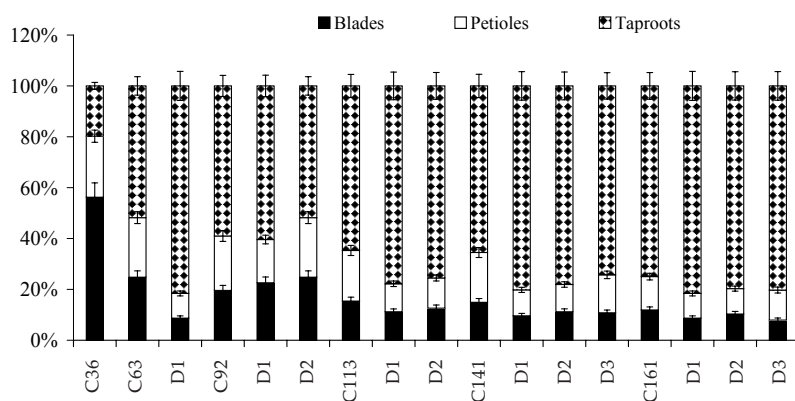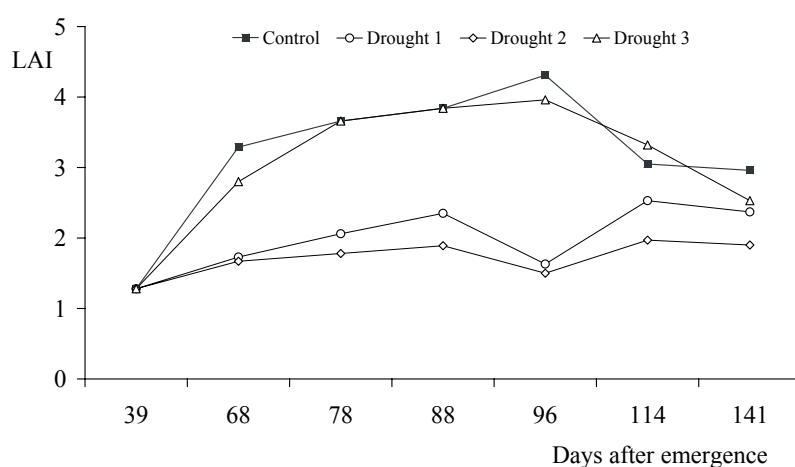
Figure 2. Time course of sugar beet plants dry matter (A), LAI (B) and dry matter partitioning (C) under different timing of drought treatment

Water shortage influenced both root yield and sugar yield by 16.1–51.6%, depending on the drought timing in the season (Table 3). Most severe was that imposed at root development stage (D2). Concentration of sucrose as well as the efficiency of the sugar extraction process (technological sugar) were not changed significantly in result of all drought treatments on account of some reduction in the concentration of K^+ and α-amino-N solutes, mainly when water deficit affected early growth of shoot (D1) or root (D2). Concentration of P_i significantly increased as an effect of D1 and D3

and decreased when water shortage was imposed during early growth of the roots.

DISCUSSION

The sugar beet is a plant that is agriculturally important because of its ability to store sucrose to high concentration in its taproot. The yield of sugar in the taproots is the product of the total amount of dry matter accumulated during growth, the proportion allocated to the storage root, and

the proportion of the taproot dry matter accumulated as sucrose (Bell et al. 1996). In addition, the efficiency of the sugar extraction process is dependent on the concentration of solutes other than sucrose (K$^+$, Na$^+$, amino acids and glycine betaine) and the interrelationships among accumulation of sucrose and these so-called impurities are important determinants of root quality. Our aim here was to investigate the drought effect on the final yield and quality on aspects of plant growth and assimilate partitioning.

Cessation of watering for a period at least 27days at different stage of plant development, imposed moderate water stress and resulted in the reduction of the RWC of young and old leaves as demonstrated previously by Clarke et al. (1993), and Kevrešan et al. (1997/1998). It is declined by about 3–6%, which corresponded to decrease in leaf water potential of 0.2–0.3 MPa from –0.8 to –1.0 MPa – calculated according to Milford and Lawlor (1976). Nevertheless, water status of mature leaves was unaffected by water shortage. Relative water content of well-watered leaves altered from 85 to 97% and was dependent on the stage of leaf and plant development. Young leaves generally contained less water than mature and old ones, probably due to different behaviour of their stomata in response to changes in leaf water potential (data will be presented in accompanying paper). As it was previously stressed by Cavazza and Patruno (1993) and also by Milford and Lawlor (1976), stomata of young leaves are much less sensitive to vary in ψ_w than those of mature ones. At ψ_w = –1.0 MPa stomatal conductance in young leaves was almost three times greater than that of mature leaves at the same potential. We also observed the different wilting pattern of young and an older leaf, which was earlier, underlined by those authors.

However, all individual organs of sugar beet plants contained significantly less water when drought stressed. A more severe reduction was denoted in roots than in the shoots, mainly when water stress was imposed at foliar development. Nevertheless, during recovery time, water status of shoot still maintained at lower level in plants earlier subjected to drought in comparison to well-watered ones what was in contrast to the taproot response. Overall, data concerning the different water status in plant organs in response to water stress implies that a hydrodynamic equilibrium does not exist within the sugar beet plant. Sugar beet posses an effective mechanism for osmotic adjustment both in the shoot (McCree and Richardson 1987, Gzik 1996) and in the root tissue (Shaw et al. 2002). The osmotic potential decreased sufficiently in the both kind of tissues so that turgor remained constant as the plants became water deficient which was shown in maize (Westgate and Boyer 1985, Hsiao
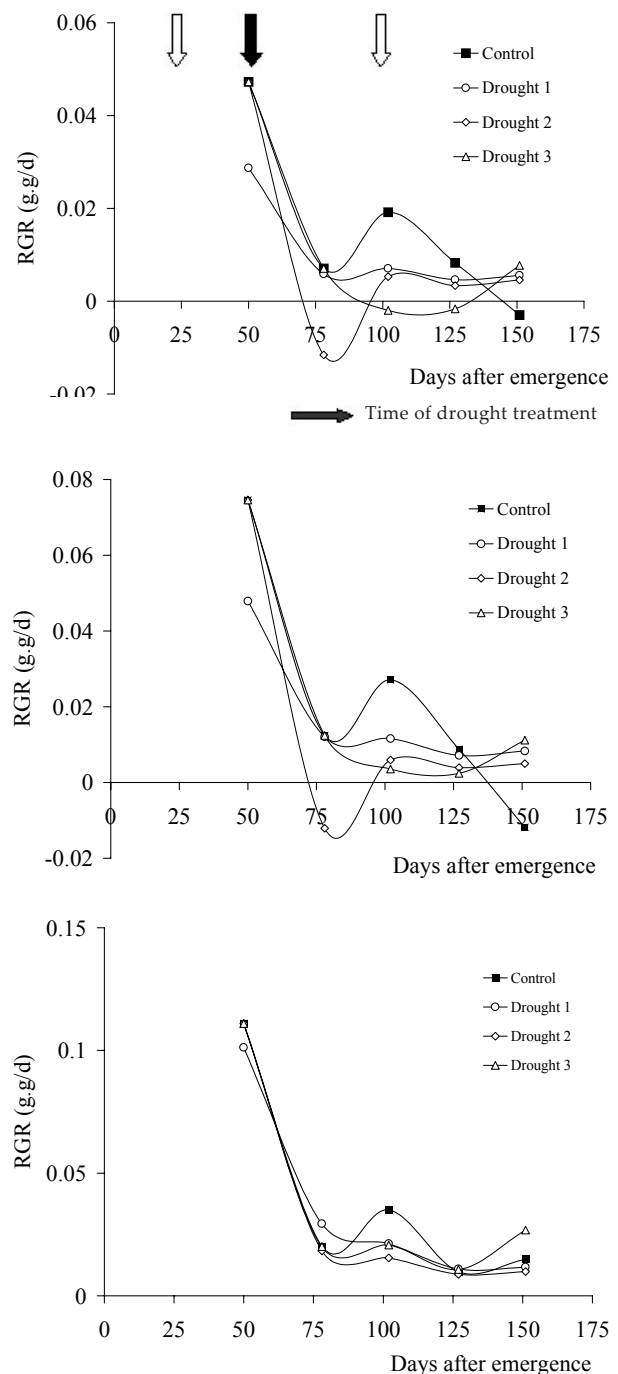

Figure 3. Time course of RGR of sugar beet blades (A), petioles (B) and taproots (C) under different timing of drought treatment

2000) and the young sugar beet leaves (Milford and Lawlor 1976, and our observation about wilting response). Hsiao (2000) suggested that root tissue possessed higher capacity of osmotic adjustment and turgor maintenance at low ψ_w than the shoot. This supposition could explain our data concerning lower water content and higher dry matter accumulation in young leaves and roots

Table 2. Effect of 27 days drought stress on the root to shoot ratio of sugar beet plants

DAE	63			92			141		
	control	D1	*LSD*	control	D2	*LSD*	control	D3	*LSD*
	1.07	**1.52**	0.18	1.44	**2.50**	0.16	1.89	**2.88**	0.13
161 DAE	control	D1			D2			D3	*LSD*
	2.99	**4.43**			**3.93**			**4.06**	0.06

of drought stressed sugar beet plants. The idea, that the taproots and younger leaves of sugar beet plants adjust osmotically more quickly than older leaves will be prove in next paper. When water was withheld, gradient of water potential disappeared in the leaves preventing water transport from the xylem to the mesophyll cells but in the roots, the gradient did not decreased (Westgate and Boyer 1985). Therefore, the gradient in ψ_w would favour water uptake by the root, but not leaves at low water supply. In result, after stress cessation root water status recovered faster than that of the shoot which showed our data.

Water withholding reduced plant growth, dry matter accumulation and final yield when imposed at successive growth stages, which was partially compensated by an increase in the fraction of assimilate partitioned to storage. Nevertheless, its response was most severe when stress affected foliar development. This is in accordance with results reported by Bazza (1993). One of the reasons of this different final yield response is the higher ability to recovery of the whole plant growth in conditions when drought occurs at the end of crop cycle, which sowed our RGR data.

However, growth of sugar beet leaves was highly sensitive to inhibition by water stress than that of taproots. It was previously demonstrated for sugar beet (Abdollahian-Noghabi and Froud-Williams 1998, Werker et al. 1999, Shaw et al. 2002) and other species (Hsiao 2000) that there is a sharp contrast between the root and the leaf in their growth responses to water deficit. In our experiments, its impact was different depending on the time of drought treatment. The hampering of leaf area caused by temporary drought imposed at early phase of plant development is in accordance with data of Bazza (1993) and Clover et al. (1999). Generally, the rate of growth depends in others on the maintenance of turgor for extending the cell walls and the presence of ψ_w gradients for supplying water to the growing regions. In the taproots and probably in the young sugar beet leaves high ability to maintenance of turgor and ψ_w gradients under moderate water deficit allowed their growth to continue. This contrasting growth behaviour within the plant might affect dry matter accumulation less in the taproot than in the shoot. Therefore, a rapid and about 1.5 times increase in the root/shoot ratio was observed in water limited conditions. Nearly the same range was reported by Show et al. (2002). At the end of crop cycle, after different periods in the recovery processes, the amount of dry matter allocated to the storage was still higher in drought stressed plants.

The root quality of the sugar beet, especially inorganic cations and phosphorus and N compounds concentration are usually affected by drought imposed during growth (Bell et al. 1996). Consequently, concentrations of sugar and α-amino-N are usually negatively correlated and it has been suggested that this be because the accumulation of N-compounds in beet cells precludes that of sucrose (Shore et al. 1982). In

Table 3. Yield response of sugar beet to different timing of drought

Treatment	Root yield		Sugar yield (kg/m²)	Concentration					Technological sugar (%)
	(kg/m²)	(%)		sugar (%)	K	Na	α-amino-N	inorganic P (mmol/kg DW)	
						(mmol/kg FW)			
Control	9.11	**100.0**	1.51	19.5	68.1	3.8	17.7	173.7	16.5
D1	4.76	**52.3**	0.81	19.5	56.7	3.4	9.5	193.3	17.0
D2	4.41	**48.3**	0.74	19.2	57.3	3.8	10.1	159.1	16.7
D3	7.64	**83.9**	1.24	19.0	66.9	3.8	12.1	186.9	16.2

our experiments, drought stress did not change the sugar content as demonstrated previously by Rover and Buttner (1999) as an effect of periodical and permanent reduction of water supply. Water shortage, which occurred at foliar and early stage of root development, decreased the contents of important non-sugar compounds and therefore only slightly increased the sugar in molasses.

Acknowledgement

Abbreviations

DAE – days after emergence
KHBC Ltd. – Kutnowska Sugar Beet Breeding Company
LAI – leaf area index
RGR – relative growth rate
RWC – relative water content
Ψ_w – water potential

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ABSTRAKT

Růst a rozdělení sušiny v cukrovce (*Beta vulgaris* L.) při mírném suchu

Byl zkoumán negativní vliv sucha na kvantitu a kvalitu výnosu cukrovky růstovou odezvou na stres ze sucha, působícího v rozdílných stadiích růstu: rozvoj listů (4. až 5. list) nebo začátek vývoje kořene a intenzivní akumulace v kořeni. Přerušení zavodňování vynutilo mírný vodní stres a rezultovalo v redukci relativního obsahu vody (RWC) mladých a starých listů. Údaje vztahující se k rozdílnému stavu vody v orgánech rostliny a listech znamenají, že hydrodynamická rovnováha v rostlinách cukrovky jako odpověď na vodní stres neexistuje. Nedostatek vody redukuje růst rostliny, akumulaci sušiny a konečný výnos, je-li vyvolán v následném období růstu, které bylo částečně kompenzováno vzrůstem v části přizpůsobené k ukládání. Odpověď cukrovky byla nejsilnější, když stres ovlivnil foliární vývoj. Stres ze sucha nezměnil obsah cukru, pokud se však objevil ve foliárním raném období rozvoje, snížil obsah významných necukerných sloučenin, takže pouze nepatrně redukoval cukr v melase.

Klíčová slova: *Beta vulgaris* L.; sucho; distribuce sušiny; růst; plocha listu; obsah vody; kvantita a kvalita výnosu

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