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Genotypic response to re-growth of defoliated sugar beets after re-watering in a water-limited environment: effects on yield and quality

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Abstract

Defoliation produced by abiotic factors and the subsequent re-growth can reduce sugar beet (*Beta vulgaris* L.) sucrose content and final sugar yield. Field experiments were conducted during 2003 and 2004 growing seasons in the farm of Hellenic Sugar Industry SA, Larissa factory, central Greece. Three sugar beet cultivars (*Rival*, *Europa* and *Corsica*) were ordinary irrigated till the beginning of July and then left without irrigation for a month. Three defoliation levels (control-C, moderate-MD and severe-SD) were performed at early August and irrigation was simultaneously started to promote re-growth. Four samplings were conducted (before defoliation, 15, 30 and 40 days after defoliation) to determine the changes in physiological and productive traits. Yields were lower in 2003 compared to 2004 because sugar beets were grown under more stressful conditions due to the delayed sowing, the higher temperatures and the lower rainfall. Both defoliation level and cultivar had significant effects on physiological and productive traits after re-growth only in 2003. The late-season cultivar, *Corsica*, showed better LAI maintenance compared to *Europa* and *Corsica* and had the greatest performance after re-growth in regard to fresh root weight and sugar yield. Also, this cultivar showed the least decrease of sucrose percentage in fresh root weight and juice purity mainly due to the stable potassium (K) concentration and limited increase of sodium (Na) accumulation in roots. *Corsica* consumed the least root α-amino N for its re-growth. Quantitative and qualitative traits were negatively affected only by the SD treatment. Plants suffered from MD treatment gradually recovered during growing season. This study demonstrates that under Mediterranean conditions, the adverse effects of re-growth on sugar beet yield and quality depend on the growing conditions and they can be restricted by the selection of an appropriate cultivar.

Keywords: *Beta vulgaris* L; Defoliation; Drought; Semi-arid environments.

Introduction

Sugar beet (*Beta vulgaris* L.) is considered as both drought and salinity tolerant species (Francois and Maas, 1994) but even moderate water deficits have negative impacts on crop productivity (Abdollahian-Noghabi and Froud-Williams, 1998; Choluj et al., 2004). Due to the expected expansion of the semi-arid conditions to the central and northern Europe as a consequence of the climatic change (Jones et al., 2003); drought tolerance of sugar beet has recently gained great interest (Sadeghian et al., 2000; Ober et al., 2005; Pidgeon et al., 2006).

Under semi-arid, Mediterranean conditions of central Greece, water is the main constraint of sugar beet productivity and supplemental irrigation of ~550 mm is necessary to secure crop profitability (Analogides, 1993). Since it is common for growers to give priority to the irrigation of cotton, which is the major spring crop in the region, irrigation water is not always available for sugar beet. Thus, in July and August when water demand is maximum, sugar beets are grown under water deficit conditions.

As a Chenopodiaceae, sugar beet has evolved leaf loss (defoliation) and re-growth after re-watering as a mechanism to cope with the summer drought on the clayey-saline soils where it grows (Vesk and Westoby, 2003). This is the case in central Greece where prolonged water stress is followed by irrigation or rainfall at the end of summer. The restoration of water supply after a prolonged water stress period can have detrimental effects on sugar beet productivity due to harmful changes in plant physiology (Owen and Watson, 1956). Foliage losses and consequently photosynthetic machinery losses retard sugar beet growth. Defoliated plants depend on stored material in roots to cover their maintenance and growth costs till the re-establishment of a positive energy budget by restoring their canopy. Re-growth of biennial and perennial species is the result of the degradation of root storage proteins, which provide the necessary N supply (Avice et al., 1997; Bewley, 2002). In re-grown plants, newly expanded leaves seem to be more photosynthetic ally active than the older ones (French and Humphries, 1977; Carter et al., 1978) and can eliminate yield losses due to the consumption of stored material in roots (Afanasiev, 1964). In central Greece, field observations by growers and agronomists demonstrated that sugar beet cultivars respond differently to re-watering after stress-induced defoliation. The differences are expressed by the degree of canopy restoration and changes in yield and quality. An ideal response should be a quick restoration of canopy up to the optimum LAI (~3-4), negligible root weight losses, no significant decrease of sucrose content and no degradation of root quality.

Although defoliation by biotic (e.g. insects) or abiotic (e.g. hail) factors and the effects of subsequent re-growth have been studied (Dunning and Winder, 1972; French and Humphries, 1977; Carter et al., 1978; Sands, 2001), we are unaware of any work on sugar beet aiming to simulate re-growth of water stressed sugar beets after water restoration. Thus, three sugar beet cultivars (*Europa*, *Rival*, *Corsica*) were subjected to three defoliation levels (control-C, moderate-MD and severe-SD). Physiological (Leaf Area Index and chlorophyll content), quantitative (fresh root weight, sugar yield and dry root weight) and qualitative (sucrose percentage in fresh and dry root weight, K, Na, α-amino N and juice purity) measurements were performed once before re-growth and three times after re-watering (15, 30 and 40 days after defoliation).

Materials and Methods

Experimental site, set up and treatments

Three sugar beet cultivars (*Rival*, *Europa*-SESVANDERHAVE NV/SA, Tienen, Belgium, and *Corsica*-Maribo, Danisco Seed, Holefy, Denmark) were grown during 2003 and 2004 growing seasons in the farm of Hellenic Sugar Industry SA, Larissa factory, central Greece (39º 43' N, 22º 28' E, 76 m above sea level). Table 1 presents soil characteristics and Figure 1 displays meteorological data of the experimental site for the two growing seasons of experimentation. *Europa* is an early-harvested cultivar; *Rival* is a mid-season and *Corsica*, a late-season one. Three defoliation levels (control-C, moderate-MD and severe-SD) were simulated in each cultivar. The experimental design was a split-plot with four replications when cultivars were in the main plots and defoliation levels in the sub-plots. Seeds were mechanically drilled (Hege 80, Wintersteiger AG, Ried, Austria) in rows with 8 m length, 45 cm apart and at 9.1 cm spacing in the row. Each plot consisted of twelve rows. While in 2003, winter rainfall delayed sowing (17 April), it did not repeat in 2004 (18 March). Based on soil analysis before sowing, adequate fertilization was provided as basal and top-dressing (150 kg N ha^{-1} and 90 kg P ha^{-1}). At the stage of 2-true leaves, hand thinning was done to achieve a population of ~100000 plants ha^{-1}. Full protection against weeds, insects and fungi (cercospora and powdery mildew) was taken by applying appropriate pesticides.

Table 1. Soil characteristics before the establishment of the experiments.

Depth	Sand	Silt	Clay	pH	Total $CaCO_3$	Organic matter	CEC	Total N	NO_3-N	P-Olsen	Exch-K	Exch-Na
(0-30 cm)	($g\ kg^{-1}$)			(1:1)	($g\ kg^{-1}$)		($cmol\ kg^{-1}$)	($g\ kg^{-1}$)	($mg\ kg^{-1}$)			
2003	180	290	530	8.3	27.0	9.2	34.5	1.17	6.2	5.2	295	123
2004	150	230	620	8.3	19.0	12.7	37.6	1.28	9.2	6.9	289	224

CEC, Cation Exchange Capacity

Supplemental irrigation was given till the beginning of July (a total of 250 mm water), and then sugar beets were left without irrigation for a month. At early August, three defoliation treatments were applied (control-C, moderate-MD and severe-SD). MD plants were defoliated by hand to leave only the newly expanded leaves (~25% of the LAI of C plants) and SD plants were left only with the meristematic leaves (LAI ~0). Immediately after defoliation, irrigation (~ 70 mm) was started to promote re-growth.

Samplings and determinations

Four samplings were conducted to determine the quantitative and qualitative traits. First sampling took place on 10th August, before defoliation, in C plots of each cultivar. Three samplings followed 15, 30 and 40 days after defoliation (DAD). In each plot, two internal rows (6.3 m^2) were harvested by hand. Sugar beets were topped by hand and the number of roots was counted. Fresh roots were immediately weighed and a sub-sample of 25-30 roots was transferred to the factory's tare house for root quality measurements (sucrose percentage in fresh root weight-SC, K, Na and a-amino N contents), which were conducted using a Venema automatic beet laboratory system (Venema automation b.v., Groningen, Holland) connected with a BETALYSER® analysing system (Dr Wolfgang Kernchen GmbH, Seelze, Germany). Root K and Na concentrations were measured by flamephotometry and α-amino N was determined by TESTAMIN digital photometer with the blue number method. Impurities were expressed in meq 100 g^{-1} fresh root weight and transformed to mg $100g^{-1}$ sucrose. Root juice purity (JP) was estimated using the formula of Reinfeld et al. (1974). Root water content was estimated by comparing fresh and dry weights of a root sub-sample (~200 g fresh weight) taken from two, randomly selected roots in each plot. Sugar yield (SY) was estimated by combining fresh root weight (FRW) and SC.

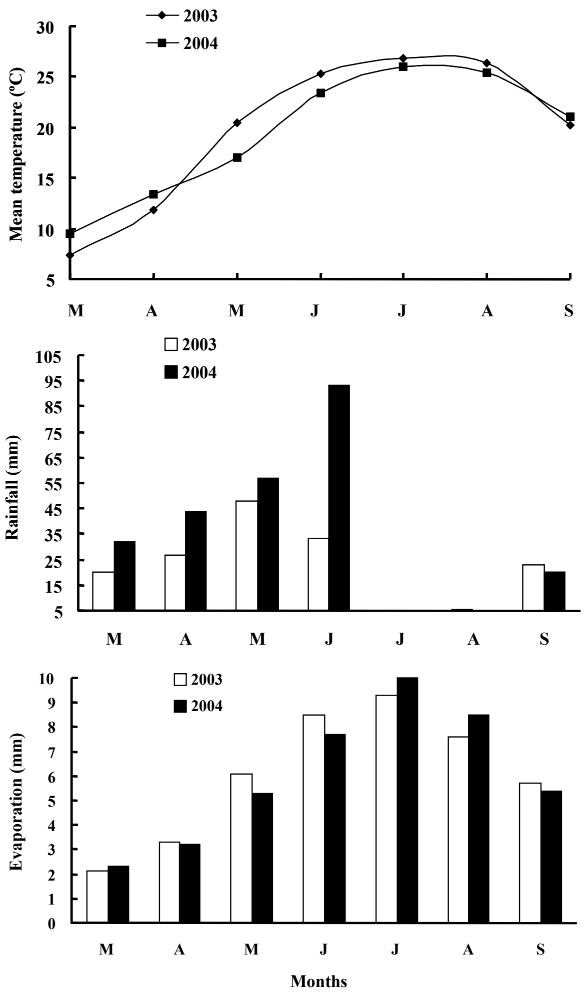

Figure 1. Seasonal trends of the mean monthly temperature (ºC), monthly rainfall (mm) and mean monthly evaporation (mm).

Before root harvest, in each plot, leaf chlorophyll content and Leaf Area Index (LAI, leaf area, in m^2, per m^2 ground) were determined. Chlorophyll content was assessed non-destructively using SPAD-502 (Minolta Co, Osaka, Japan) on ten upper, full-expanded, intact, and full sun-lit leaves. For LAI determination, two measurements per plot were taken using the SunScan system (Delta-T Devices Ltd, Cambridge, UK).

Statistical analysis

Data of the physiological and productive traits in the C plots, determined before re-growth, were analyzed as a Randomized Complete Block design combined over years with cultivars as main factor. In order to evaluate the performance of each cultivar across years and samplings towards a common base (Bilbao et al., 2004), the data of the samplings after re-growth were transformed to relative values (the ratio of each trait value to the respective cultivar C mean before re-growth). The relative values were subjected to Analysis of Variance (ANOVA) and the means were compared with the Least Significance Difference (LSD) test at P<0.05 using the M-STAT statistical package (MSTAT-C, version 1.41, Crop and Soil Sciences Department, Michigan State University).

Results

Physiological, quantitative and qualitative traits in the C plots before defoliation

SPAD readings were affected by year, cultivar and their interaction (Table 2). Higher SPAD readings were found in 2003 compared to 2004. Over years, *Corsica* had the higher SPAD (46.6) compared to *Europa* and *Rival* (42.9 and 42.7, respectively). LAI combined over cultivars was higher in 2004 (2.2) compared to 2003 (1.7). Cultivars differed significantly regarding LAI in 2003 when *Corsica* showed the lowest values (Table 2).

Table 2. Physiological, quantitative and qualitative traits of the three cultivars before re-growth for the two years of experimentation. In each column, means labelled with the same letter did not differ significantly at P<0.05. In columns without labelling, no significant differences between means were found.

Cultivars	SPAD	LAI	RFW	SC	SY	K	Na	a-amino N	JP	RDW	DSC
	units		t ha^{-1}	%	t ha^{-1}	mg 100 g^{-1} sugar			%	t ha^{-1}	%
						2003					
Europa	45.72b	1.94a	38.85c	16.24	6.38c	1207	495.4	189.0bc	81.98	9.14c	65.27
Rival	43.80bc	2.03a	32.08d	16.80	5.40cd	1158	587.1	199.1bc	81.46	8.58cd	65.16
Corsica	50.69a	0.98b	26.11e	16.65	4.35d	1060	652.7	147.7c	82.77	6.59d	62.25
						2004					
Europa	40.11d	2.33a	59.59a	16.45	9.67a	1201	479.5	298.6a	81.37	14.03a	69.55
Rival	41.54cd	2.32a	46.79b	17.51	8.18b	1141	441.8	287.4ab	82.52	11.66b	71.06
Corsica	42.43cd	2.08a	57.89a	17.09	9. 90a	949.2	452.5	278.8ab	83.62	13.66ab	72.57
CV (%)	4.61	22.70	8.05	4.53	9.67	16.78	34.81	27.60	2.58	13.48	11.92

LAI, Leaf Area Index; RFW, root fresh weight; SC, sucrose percentage in fresh root weight; SY, sugar yield; JP, juice purity; RDW, root dry weight; DSC, sucrose percentage in root dry weight; CV, coefficient of variation

Both years, in all plots, root number was higher than 75000 plants ha^{-1}, the threshold level for maximum yield (data not shown). Significant year × cultivar interactions were found for RFW, (SY) and root dry weight (RDW), which were higher in 2004 compared to 2003. *Corsica* and *Rival* had the lowest yields (RFW, SY, and RDW) in 2003 and 2004, respectively. Year and cultivar had no significant effect on sucrose content in fresh root weight (SC) (Table 2).

Juice purity (JP), K and Na concentration in roots were not affected by the main factors (year and cultivar) and their interaction. Higher α-amino N concentration in roots was found in 2004 compared to 2003. Combined data over cultivars, percentage of sucrose in root dry weight (DSC) was significantly higher in 2004 (71.1%) compared to 2003 (64.2%) (data not shown). No significant cultivar effect on the DSC was evident.

Response of the physiological traits to re-growth

Table 3 presents the ANOVA results for the physiological and productive traits after re-growth. With the exception of Na concentration in roots, year affected significantly all the traits. SPAD readings combined over years, cultivars and defoliation level increased by 15 DAD, reached a minimum after 30 DAD and increased again by 40 DAD (Figure 2A).

Table 3. Results of the Analysis of Variance (ANOVA) for physiological, quantitative and qualitative traits of the three cultivars after re-growth for the two years of experimentation.

Source	df	SPAD	LAI	RFW	SC	SY	K	Na	amino-N	JP	RDW	DSC
Years (Y)	1	***	***	***	***	***	***	ns	**	***	***	***
Defoliation(D)	2	ns	***	*	***	***	*	***	ns	***	***	*
Y×D	2	ns	***	ns	*	**	ns	**	ns	***	**	ns
Cultivars(C)	2	ns	***	***	*	***	***	**	**	**	***	ns
Y×C	2	ns	***	***	ns	***	ns	*	**	ns	**	ns
D×C	4	ns	**	ns	ns	ns	ns	ns	*	ns	ns	ns
Y×D×C	4	ns	*	ns	ns	ns	ns	ns	ns	*	ns	ns
Samplings (S)	2	**	***	**	***	***	***	***	***	***	***	ns
Y×S	2	ns	***	ns	***	***	***	**	*	**	**	***
D×S	4	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns
Y×D×S	4	ns	**	ns	**	**	ns	*	ns	**	ns	ns
V×S	4	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Y×C×S	4	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
D×C×S	8	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Y×D×C×S	8	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CV (%)		8.60	36.04	15.73	6.72	16.29	18.57	27.56	30.73	3.82	17.56	9.56

df, degrees of freedom; CV, coefficient of variation; LAI, Leaf Area Index; RFW, root fresh weight; SC, sucrose percentage in root fresh weight; SY, sugar yield; JP, juice purity; RDW, root dry weight; DSC, sucrose percentage in dry root weight, ns, not significant. *P<0.05, ** P<0.01, *** P<0.001.

After re-growth, LAI development depended on defoliation level (Figure 2B) and cultivar (Figure 2C). Fifteen DAD, LAI of the C plants increased by 3% and then decreased gradually till the end of the season. In the MD plants, LAI increased by 35% (60% minus 25% LAI left after defoliation) in 15 DAD and remained stable thereafter. SD plants increased LAI gradually till 30 DAD by ~50% (LAI left after defoliation in this treatment was practically 0) and then LAI declined.

Cultivars responded differently to re-growth (Table 3 and Figure 2C). In the MD and SD plants, *Corsica* increased LAI more than *Europa* and *Rival*. Combined LAI over years and samplings, non-significant differences were found between C and MD plants in *Corsica*.

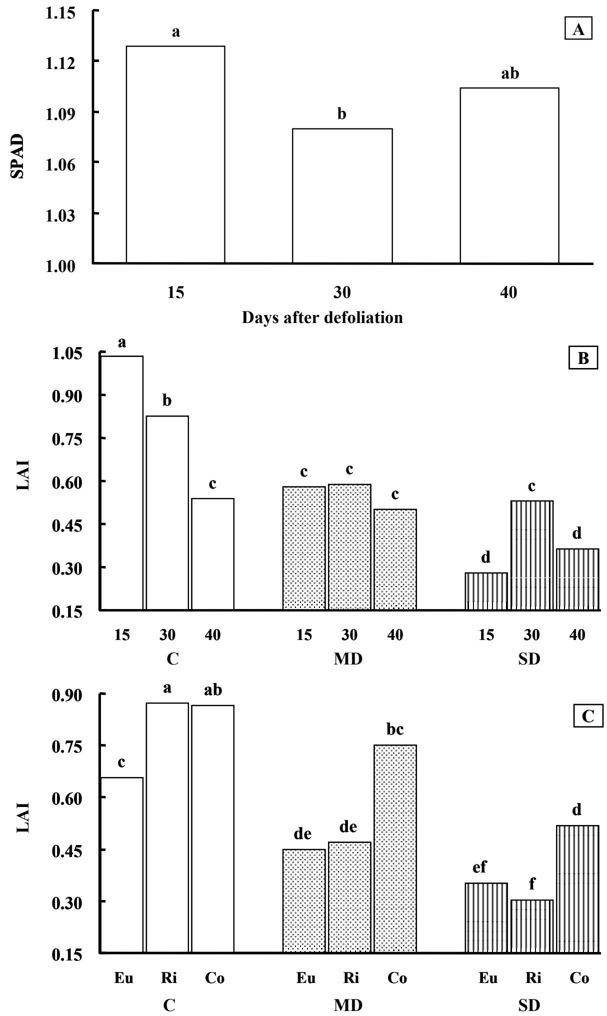

Figure 2. Defoliation effect on SPAD (A) and significant defoliation × sampling (B) and defoliation × cultivar (C) interactions for LAI after re-growth. Columns superscript with the same letter did not differ significantly at P<0.05. Eu, *Europa*; Ri, *Rival*; Co, *Corsica*; C, control; MD, moderate defoliation; SD, severe defoliation.

Response of RFW, SC and root quality to re-growth

RFW increase was inversely related to the defoliation intensity (Figure 3A). The C plants increased RFW by 41% after re-growth while the increase was only 31.8% in SD plants. A significant year × cultivar interaction was evident for RFW (Figure 3B). RFW increased less in 2004 compared to 2003. Although cultivars did not differ significantly in 2004 (*Europa*: 31%, *Rival*: 26.5%, *Corsica*: 23.3%), *Corsica* and *Europa* (63.8% and 54%, respectively) showed the higher FRW increases compared to *Rival* (23.5%) in 2004. No significant difference between years was found for *Rival* (23.5% and 26.5%, respectively). RFW increased gradually by 30 DAD and then remained constant (Figure 3C).

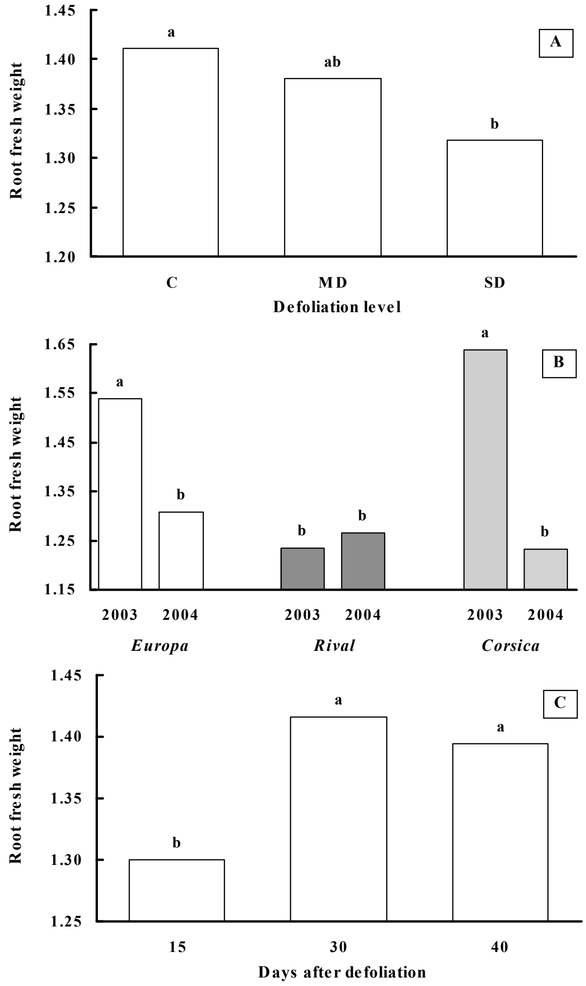

Figure 3. Effects of defoliation (A), year × cultivar interaction (B) and sampling (C) on fresh root weight after regrowth. Columns superscript with the same letter did not differ significantly at P<0.05. C, control; MD, moderate defoliation; SD, severe defoliation.

Corsica showed lower reduction of SC (13.6%) compared to *Rival* and *Europa* (16% and 15.7%, respectively) (Figure 4A). A decline of SC with defoliation level was evident but it was more pronounced in 2003 (Figure 4B). In 2003, SC recovered with DAD and only a 7% reduction was evident 40 DAD. SC followed different patterns between years. In 2004, SC was highest in 15 DAD (-12.7%), lowest in 30 DAD (-20.5%) and moderate at 40 DAD (-16.2%) (Figure 4C).

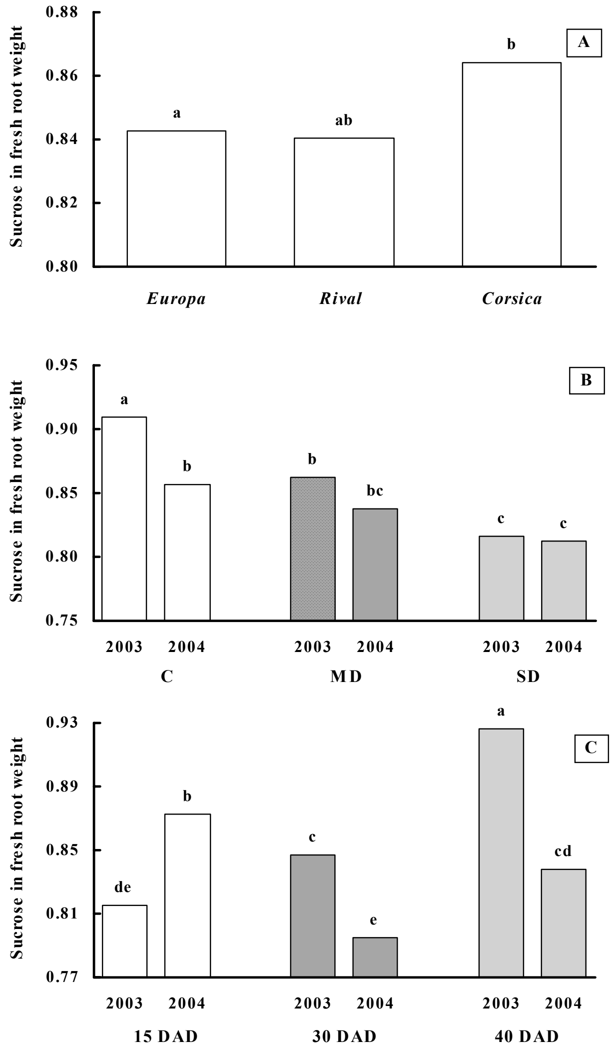

Figure 4. Effects of cultivar (A), year × defoliation (B) and year × sampling (C) interactions on sucrose percentage in fresh root weight after re-growth. Columns superscript with the same letter did not differ significantly at P<0.05. C, control; MD, moderate defoliation; SD, severe defoliation; DAD, days after defoliation.

Combined data over cultivars, samplings and defoliation level, sugar yield (SY) increased by 30% in 2003 but only by 10% in 2004. Year affected significantly the response of SY to defoliation level, cultivar and sampling (Table 3). Significant differences were found only in 2003 (Figure 5). Increases of SY were higher in C and MD plants (39.1% and 30.3%, respectively) compared to SD plants (11.6%) (Figure 5A). *Corsica* showed the highest SY increase (44.5%) followed by *Europa* (29.9%) and *Rival* (6.6%)

(Figure 5B). SY increased gradually with the progress of the growing season and the highest SY increase was evident at 40 DAD (Figure 5C).

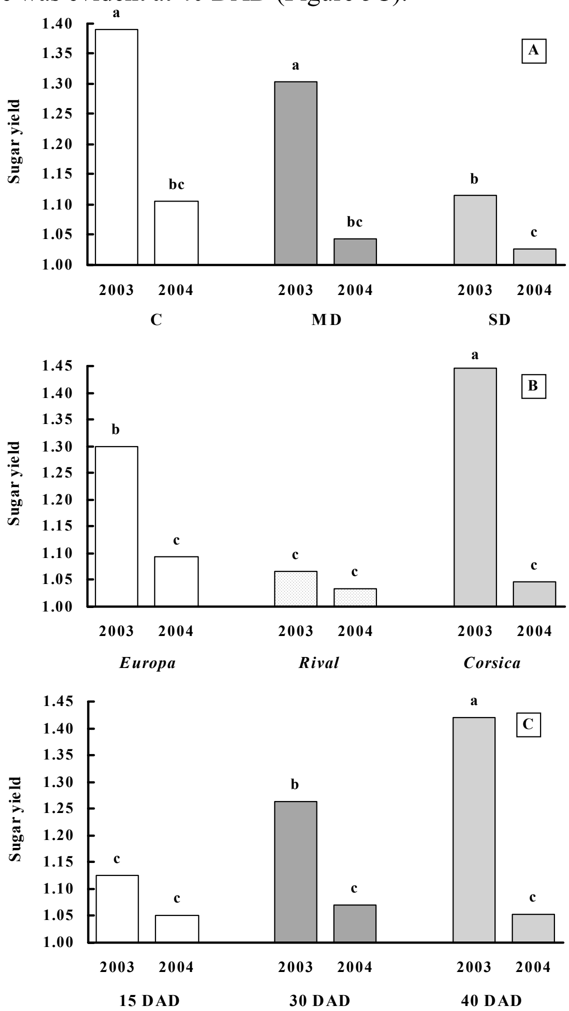

Figure 5. Effects of year × defoliation (A), year × cultivar (B) and year × sampling (C) interactions on sugar yield after re-growth. Columns superscript with the same letter did not differ significantly at P<0.05. C, control; MD, moderate defoliation; SD, severe defoliation; DAD, days after defoliation.

Corsica had almost constant K concentration in roots (-0.5%) while the other two cultivars showed significant increases (*Europa*: 32.1% and *Rival*: 26.5%) (Table 4). Defoliation level affected positively K in roots, especially the SD treatment. Sampling time and defoliation level affected positively Na concentration in roots. *Europa* showed the highest increase of Na in roots (Table 4). *Corsica* showed the smallest decrease of α-amino N in both years (Table 4). In 2003, α-amino N in *Rival* and *Europa* decreased by ~35% and

25%, respectively. The α-amino N concentration decreased with DAD especially in 2004 (data not shown). Juice purity (JP) was less reduced in *Corsica* and *Rival* (-3% and -3.5%, respectively) compared to *Europa* (-4.75%). A significant effect of defoliation on JP was found only in 2003 when JP decreased with the increased defoliation level (Table 4). It is characteristic that JP of the C plants was not affected by re-growth in 2003.

Response of RDW and DSC to re-growth

Defoliation level affected significantly the increase of RDW. In both years, the SD plants showed the lowest RDW increases (1-3%) and the C plants the highest increases (2003: 35% and 2004: 16%). The RDW increased significantly with the DAD and the trend was more pronounced in 2003. No cultivar effect on RDW was found in 2004 but *Europa* and *Corsica* showedd the highest RDW increases in 2003 (26.1% and 31.5%, respectively) (Table 5).

Table 4. Comparison of means of the root impurities (K, Na and α-amino N) and juice purity (JP) after re-growth for cultivars and the significant year×defoliation interaction. In each comparison, means labelled with the same letter did not differ significantly at P<0.05.

	K	Na	α-amino N	JP
Cultivar				
Europa	1.32a	1.70a	0.81b	0.95b
Rival	1.27a	1.53b	0.75b	0.97a
Corsica	0.99b	1.43b	0.91a	0.97a
Year × Defoliation				
2003				
C	0.92b	1.21c	0.81	1.00a
MD	0.99b	1.50b	0.79	0.98b
SD	1.12ab	1.80a	0.72	0.95c
2004				
C	1.36a	1.59b	0.91	0.95c
MD	1.37a	1.56b	0.81	0.96c
SD	1.39a	1.66ab	0.88	0.95c

C, control; MD, moderate defoliation; SD, severe defoliation

DSC was positively affected by defoliation intensity (Figure 6A). Although DSC decreased by 1% in the C plants, it increased by 0.9% and 3.5% in MD and SD plants, respectively. A gradual but not significant decrease of DSC was evident in 2004. In 2003, DSC increased by 9.8% in 30 DAD but in 40 DAD, was restricted to 4.6% (Figure 6B).

Table 5. Comparison of means of root dry weight (RDW) after re-growth for the significant interactions between year and the main factors (defoliation level, sampling and cultivar). In each interaction, means labelled with the same letter did not differ significantly at P<0.05.

	RDW
Year × Defoliation	
2003	
C	1.35a
MD	1.26ab
SD	1.01c
2004	
C	1.16ab
MD	1.06c
SD	1.03c
Year × Sampling	
2003	
15 DAD	1.11bc
30 DAD	1.15b
40 DAD	1.36a
2004	
15 DAD	1.05c
30 DAD	1.10bc
40 DAD	1.10bc
Year × Cultivar	
2003	
Europa	1.26a
Rival	1.05b
Corsica	1.32a
2004	
Europa	1.11b
Rival	1.06b
Corsica	1.08b

C, control; MD, moderate defoliation; SD, severe defoliation; DAD, days after defoliation

Discussion

Water shortage is the main constraint of sugar beet productivity in central Greece. Limited rainfall and irrigation water during July and August force sugar beets to grow under water deficit conditions imposing foliage loss (defoliation), which is a mechanism of adaptation (Vesk and Westoby, 2003).

In 2003, the delayed sowing, the higher temperatures and the lower rainfall subjected sugar beets to an earlier and more severe drought. This effect was expressed by lower LAI and higher SPAD values (Tsialtas and Maslaris, 2008) and by lower yields (Mohammadian et al., 2005). The late-season cultivar, *Corsica*, was more affected by the stressful conditions as it was indicated by physiological (lowest LAI, highest SPAD) and productive (lowest FRW, SY and RDW) traits. Under the less stressful conditions of 2004, *Rival* had the lowest yields. This genotypic differentiation in regard to physiology and yield under various growing conditions is in contrary to previous reports (Bloch et al., 2005; Hoffmann et al., 2009) and it is interesting in selecting drought tolerant sugar beet genotypes (Tsialtas and Karadimos, 2003; Ober et al., 2005).

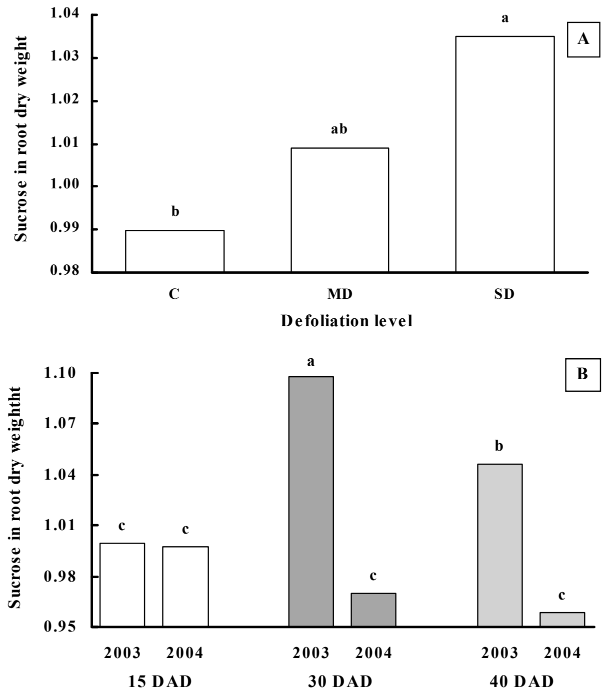

Figure 6. Defoliation (A) and year × sampling (B) effects on sucrose percentage in root dry weight after re-growth. Columns superscript with the same letter did not differ significantly at $P<0.05$. C, control; MD, moderate defoliation; SD, severe defoliation; DAD, days after defoliation.

Response to re-growth was affected by year with cultivars to be significantly differentiated in 2003 when the late-season cultivar, *Corsica*, had the highest RFW and SY increases. Due to delayed sowing in 2003, defoliation and the subsequent re-growth occurred at an earlier growth stage, which had a stronger impact on sugar beet yield (Muro et al., 1998). Under these conditions, the late-maturing *Corsica* responded better as a result of its better LAI maintenance after re-watering and re-growth, compared to *Europa* and *Rival*. A higher Leaf Area Duration (LAD) can be a critical parameter for yield formation under stressful, Mediterranean conditions (Liu et al., 2005). SPAD readings, a measure of leaf chlorophyll content and N status (Tugnoli and Bettini, 2000; Wiesler et al., 2002), showed higher values after re-growth indicating the remobilization of N to support re-growth. The C plants showed a 3% increase of LAI in 15 DAD and then foliage, following the normal physiological process, was gradually senesced. On the contrary, defoliated plants (MD and SD) re-grew intensively and almost doubled their LAI values compared to those they had just after defoliation. It is characteristic that the MD and C plants had almost equal LAI values in 40 DAD in accordance with previous reports for LAI restoration after re-growth (Abdollahian-Noghabi and Froud-Williams, 1998). However, defoliated plants had a higher percentage of newly expanded leaves, which are photosynthetically more active than the old leaves (Tsialtas et al., unpublished data). Taken into account that new leaves show lower respiration losses compared to the older ones (French and Humphries, 1977; Carter et al., 1978), the defoliated sugar beets had a better energy budget compared to the intact plants and this is a compensation mechanism, which restricted yield losses of the defoliated sugar beets (Afanasiev, 1964).

Corsica showed the smallest SC reduction after re-growth. Under Mediterranean conditions, the decline of SC during the harvesting period is a serious problem. An explanation for this reduction is the gradual restoration of water supply (irrigation or rainfall) in the course of growing season, which results to water absorption and the subsequent re-growth of water stressed sugar beets. In this context, a cultivar showing less reduction of SC after re-growth, like *Corsica*, is interesting. The SD plants showed the highest SC reduction probably as a result of the higher root water content increase (data not shown), which diluted sucrose in roots (Follett, 1991; Tsialtas and Maslaris, 2008). However, the MD plants did not differ significantly from C plants (especially in 2004) meaning that re-watering and not foliage loss was responsible for SC reduction. Reported effects of defoliation on the SC are contradictory. Carter et al. (1978) reported no significant effect of defoliation on SC but Soine (1967) found 8% SC reduction of totally defoliated sugar beets. In sugar cane (*Saccharum* spp.), the main sugar crop worldwide, partial defoliation caused non-significant decrease of SC in stems (Gutiérrez-Miceli et al., 2004).

Cultivar affected JP reduction with *Corsica* and *Rival* to be less sensitive to re-growth compared to *Europa*. Defoliation intensity had a negative impact on JP in 2003 when JP declined with the progress of DAD. *Corsica* had the smaller JP reduction as a result of the small SC losses and the lowest Na accumulation in roots compared to the other cultivars. Potassium and Na are concurrently osmotica, preventing root plasmolysis under drought and saline conditions (Stuiver et al., 1981), and root impurities, inhibiting white sugar extraction during sugar beet root processing (Harvey and Dutton 1993). Sodium is considered as the most important root impurity under Mediterranean conditions (Honarvar and Alimoradi, 2003; Tsialtas and Maslaris, 2005). In accordance with previous reports (Dunning and Winder, 1972), defoliation intensity increased the concentration of minerals in roots contributing to JP decreases. The concentration of Na and K increased with DAD in 2004, probably due to the increased amounts of water transpired by sugar beets and resulted to higher yield (Dunham, 1993).

The re-growth of biennial and perennial species after a stressful period depends on the degradation of storage proteins (Avice et al., 1997; Bewley, 2002) and the consumption of amino acids stored in taproots (Bausenwein et al., 2001; Neefs et al., 2002). In sugar beet, α-amino N is an organic N form accumulated in roots to support re-growth (Pocock et al., 1990; Bloch et al., 2006). Stressful conditions (drought, salinity, osmotic stress) promote the accumulation of α-amino N (Gzik, 1996) and concurrently decrease root quality due to the molassigenic effects of α-amino N during root processing (Harvey and Dutton, 1993). *Corsica* consumed less amino N for the re-growth due to its better LAI maintenance after re-growth. Also, *Corsica* showed non-significant differences among defoliation intensities, which was in contrary to the significant decreases with increasing defoliation found in *Europa*.

Although cultivar effects on the RDW were not significant in 2004, *Europa* and *Corsica* increased RDW more than 25% in 2003. In both years, *Rival* responded to re-growth with only 5% increase of RDW. In other tap-rooted species, consumption of photoassimilates to supply re-growth with energy is reported (Li et al., 1997; Thomas and James, 1999; Paterson and Sim, 2000; Neefs et al., 2002). On contrary, in our work, RDW of the SD plants increased by 5% or less while C plants had an increase of >15%, especially in 2003. Also, partitioning of assimilates into roots was a function of time showing the greatest increase of RDW at 40 DAD. The restricted increase of RDW in the SD plants could obviously be attributed to the consumption of compounds other than sucrose since its accumulation was increased in root dry matter. This is in contrary to findings in *Lolium perenne* in which re-watering followed by drought resulted to sugar reserves consumption in order to support re-growth (Thomas and James, 1999).

Conclusions

In 2003, sugar beets were grown under more stressful conditions due to the delayed sowing, the higher temperatures and the lower rainfalls. This was indicated by the lower LAI, the higher SPAD readings and the lower yields. Significant year × cultivar interaction was evident before re-growth with *Corsica* and *Rival* showing the lowest yields in 2003 and 2004, respectively. A significant year effect on defoliation and cultivar response to re-growth was also found. Cultivars differed significantly as regards the physiological and productive traits only in 2003. The late-season cultivar, *Corsica*, showed better LAI maintenance after re-watering, which contributed to higher increases of yield (FRW, SY and RDW), restricted SC reductions and limited JP degradation after re-growth. In regard to defoliation intensity, only SD had significant negative effects on quantitative and qualitative traits, which were the result of root stored material consumption and loss of photoassimilatory machinery as compared to C and MD plants. The MD sugar beets gradually obtained LAI values equal to those of C plants and having lower respiration cost due to higher percentage of newly expanded leaves, these plants showed productive results analogous to those of non defoliated ones.

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