Effect of defoliation on leaf physiology of sugar beet cultivars subjected to water stress and re-watering

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Abstract

Water stress causes defoliation, which can reduce yield and root quality of sugar beets (*Beta vulgaris* L.) through altered gas exchange characteristics of the leaves. In a two-year experiment, three sugar beet cultivars (*Europa*, *Rival* and *Corsica*) were subjected to three defoliation levels (control-*C*, moderate-*MD*, severe-*SD*) and re-watering after their exposition to drought for a month. Leaf physiological traits including net photosynthesis (A), transpiration rate (E), stomatal conductance (g_s), intracellular CO_2 (C_i), water use efficiency (WUE_L-A/E and WUE_i-A/g_s), leaf N concentration, petiole NO_3-N concentration, specific leaf area (SLA), leaf water potential (WP) and leaf water content (LWC), were determined before defoliation and 15, 30 and 40 days after defoliation (DAD). On contrary to previous reports, water-stressed cultivars differed significantly in their leaf physiology; the late-season cultivar *Corsica* had the lowest E and g_s values without any significant reduction in A. Thus, *Corsica* was the most water-conservative cultivar. Re-watering rapidly restored leaf physiology but a gradual decline, with the progress of DAD, was evident for A, E, g_s and C_i. After re-growth, cultivars differed only in WP and LWC with *Europa*, the early-harvested cultivar, to have the highest values. Thus, the better response (higher yield increase and lower root quality degradation) of *Corsica* to re-watering and the subsequent re-growth, as reported by Tsialtas et al. (2009), could be ascribed to its better *LAI* maintenance compared to *Europa* and *Rival* rather than to a better leaf physiological response. The *SD* plants showed the highest leaf physiological activity since they had the highest A, E, g_s and leaf N concentration. The high leaf activity and the low respiration rate are the means by which sugar beets tolerate foliage losses up to 75% and compensate yield losses after defoliation.

Keywords: *Beta vulgaris* L.; Drought; Leaf physiology; Re-growth.

Abbreviations

A: net photosynthesis; C: control; C_i: intracellular CO_2 concentration; DAD: days after defoliation; dw: dry weight; E: transpiration rate; g_s: stomatal conductance; LA: leaf area; LAI: leaf area index; LWC: leaf water content; MD: moderate defoliation; SD: severe defoliation; RGR: relative growth rate; SLA: specific leaf area; WP: leaf water potential; WUE_L: A/E; WUE_i: A/g_s.

Introduction

Productivity of sugar beets grown under semi-arid, Mediterranean conditions is mainly restricted by water availability (Morillo-Velarde and Ober, 2006). However, water scarcity is also a limiting factor in central and northern Europe and its negative effect on sugar beet productivity could be intensified in the near future due to climatic change (Jones et al., 2003).

In Mediterranean basin, rainfall during July and August, when water demands are maximized, is negligible and thus, supplemental irrigation is applied almost to the entire acreage cropped with sugar beets. In central Greece, irrigation need during the growing season is estimated to ~550 mm, a quantity not easily available (Analogides, 1993). Sugar beet, a drought tolerant species (Francois and Maas, 1994), responds to drought stress by losing part of the foliage (defoliation) to minimize its water demand (Vesk and Westoby, 2003). This is the case during the summer in central Greece where sugar beets are grown on clayey soils under water shortage conditions. In fact, the situation is more complicated since under the semi-arid, irrigated conditions, sugar beets face a combination of drought, temperature, light and salinity stresses, which can not easily distinguished (Chaves et al., 2002; Munns, 2002). Erratic rainfalls after mid-August or restored irrigation supply force sugar beets to re-grow. Re-watering after a prolonged drought period affects sugar beet physiology and yield (Owen and Watson, 1956).

Sugar beets are considered to be tolerant to defoliation since foliage losses up to 75% can be compensated and yield is not significantly affected (Afanasiev, 1964; Tsialtas et al., 2009). The selection of a suitable cultivar can also restrict root quality degradation (Tsialtas et al., 2009). It is assumed that the mechanism responsible for this compensation is that the newly expanded leaves after defoliation photosynthesize more and respire less than the older, intact leaves (French and Humphries, 1977; Carter et al., 1978). However, evidence of such mechanism in field conditions is lacking. Recently, several works were conducted to identify physiological traits for the selection of sugar beet genotypes suitable for water stress conditions (Tsialtas and Karadimos, 2003; Ober et al., 2005; Pidgeon et al., 2006). However, we are unaware of any study on sugar beet cultivar response to re-growth under Mediterranean conditions. The aim of this work was to study the leaf physiological response of three sugar beet cultivars subjected to defoliation and re-watering after drought.

Materials and Methods

Three sugar beet cultivars (*Europa*, *Rival*-SESVANDERHAVE NV/SA, Tienen, Belgium and *Corsica*-Maribo Seed International ApS, Holeby, Denmark) were grown on a clay (pH 8.3, total N 1.23 g kg^{-1}, NO$_3$-N 7.7 mg kg^{-1}, P-Olsen 6.1 mg kg^{-1}, exchangeable K 292 mg kg^{-1}, exchangeable Na 174 mg kg^{-1}) in eastern Thessaly Plain, central Greece (39º 43' N, 22º 28' E, 76 m asl) in 2003 and 2004 growing seasons. *Europa* is an early-harvested cultivar, *Rival* is mid-season and *Corsica* is a late-season one. Figure 1 presents the mean monthly temperature and monthly precipitation pattern during the growing seasons. More details on soil and climatic conditions are given by Tsialtas et al. (2009).

Seeds were drilled (Hege 80, Wintersteiger AG, Ried, Austria) in rows 8 m long, 45 cm apart and 9.1 cm spacing in the row. Each plot was consisted of 12 rows. Winter rainfalls delayed sowing in 2003 (17 April). In 2004, sowing was conducted one month earlier (18 March). Adequate fertilization was provided as basal and top-dressing (150 kg N ha^{-1} and 90 kg P ha^{-1}). No K fertilization was added due to the high soil K concentration. At the 2-leaf stage, plants were thinned by hand to achieve a population of ~100 000 plants ha^{-1}. Full protection against weeds, insects and fungi (cercospora and powdery mildew) was taken by sprayings.
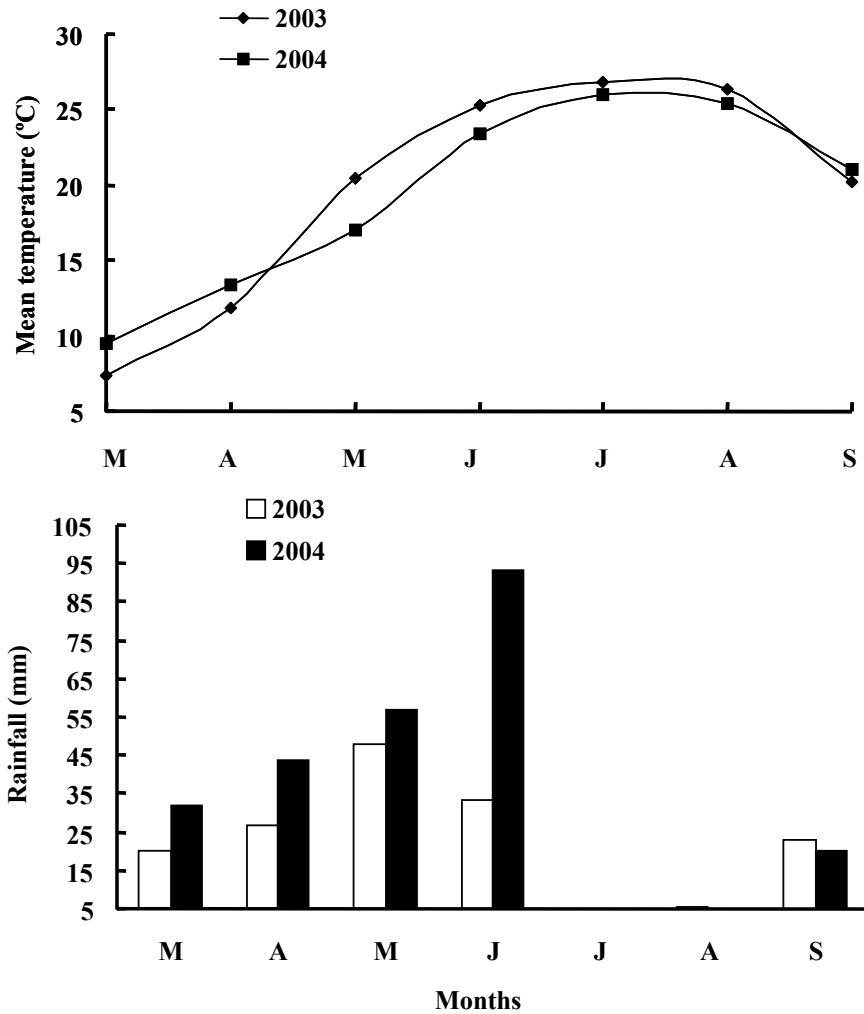
Figure 1. Seasonal patterns of mean monthly temperature and monthly precipitation during growing season.

Supplemental irrigation was given till the beginning of July (a total of 250 mm), and then sugar beets left without irrigation for a month. At early August, leaf removal treatments were applied. The three levels were control (*C*), moderate (*MD*) and severe (*SD*) defoliation. *MD* plants were defoliated to leave only the newly expanded leaves (estimated *LAI* ~25% of the *C*) and *SD* plants to leave only the meristematic leaves (*LAI* almost zero). The experimental design was a split-plot with four replications where cultivars were in the main plots and defoliation levels in the sub-plots. After defoliation, irrigation (~70 mm) was applied to enhance re-growth.

The determination of leaf physiological parameters was conducted four times; the first on 10th August (before defoliation) only in *C* plots and the others took place 15, 30 and 40 days after defoliation (*DAD*). In each plot, gas exchange (net photosynthesis-*A*, transpiration rate-*E*, stomatal conductance-g_s, intracellular CO_2 concentration-C_i) were measured in five upper, full-expanded, intact, and full sun-light leaves using LC_i portable photosynthesis system (ADC BioScientific Ltd, Hoddesdon, UK). Instantaneous water-use efficiency (WUE_L) and photosynthetic water-use efficiency (WUE_i) were estimated as *A*/*E* and A/g_s ratios, respectively.

Six leaves, similar to those used for gas exchange measurements, were collected per plot, put on an ice-chest and transferred to the Crop Physiology Lab of Larissa factory, Hellenic Sugar Industry SA. Three leaves were used for leaf area (*LA*) determinations using *WinDias* image analysis system (Delta-T Devices Ltd, Cambridge, UK) and then dried in oven at 75 °C for 48 h. Specific Leaf Area (*SLA*) was calculated as the ratio of *LA* to leaf dry weight. Leaf water content (*LWC*) was estimated by comparing fresh and dry leaf weights. Dried leaves were ground to fine powder using a microhammer cutter mill (Glen Creston Ltd, Stanmore, Middlesex, UK). Total leaf *N* concentration was measured on a *Kjeltec 2300* analyzer unit (Foss Tecator, Höganäs, Sweden). The other three leaves from each plot were used for leaf water potential (*WP*) determinations using *WP 4* system (Decagon Devices, Pullman, USA). From each plot, 10-12 petioles of upper, full-expanded leaves were collected and dried at 75 °C for 48 h. Petiole NO_3-*N* analysis, according to Johnson and Ulrich (1959), was conducted on an Orion Meter (Model 920A) using an Orion Nitrate electrode 9307 ionplus (Thermo Scientific, Nijkerk, The Netherlands).

Data of the physiological traits determined before re-growth in *C* plots, were analyzed as a Randomized Complete Block design combined over years with cultivars as the main factor. The data after re-growth were subjected to Analysis of Variance (*ANOVA*) and means were compared using Least Significant Difference (*LSD*) test at 0.05 level. The statistical analysis was conducted by *MSTAT-C* (version *1.41*, Crop and Soil Sciences Department, Michigan State University).

Results

Physiological traits in C plots before re-growth

Year did not affect leaf gas exchange parameters (*A*, *E*, g_s, C_i, WUE_L, WUE_i) but affected significantly leaf *N*, *SLA*, *WP* and *LWC* (Table 1). Leaf *N*, *SLA* and *LWC* were higher in 2003 compared to 2004 but the adverse was evident for leaf *WP* (Table 1).

Cultivars did not differ significantly for *A* (*Europa*: 13.04 μmol m^{-2} s^{-1}, *Rival*: 12.19 μmol m^{-2} s^{-1}, *Corsica*: 11.94 μmol m^{-2} s^{-1}). *Corsica* had the lowest *E*, g_s and C_i and the highest WUE_i (Table 1). No significant difference was found for WUE_L (*Europa*: 1.92 μmol mmol^{-1}, *Rival*: 1.81 μmol mmol^{-1}, *Corsica*: 2.03 μmol mmol^{-1}). *Corsica* and *Europa* had the highest leaf *N* concentration (40.6 and 39.2 mg g^{-1} *dw*, respectively) differing significantly from *Rival* (37.3 mg g^{-1} *dw*). *Europa* and *Corsica* had higher but not significant different petiole NO_3-*N* concentration compared to *Rival* (2662, 2056, 1605 mg kg^{-1} *dw*, respectively). *Europa* had higher *SLA* and *LWC* compared to *Rival* and *Corsica* (Table 1). *Corsica* showed the lowest *SLA* and *LWC* while no significant difference was found for *WP* (*Europa*: -3.79 MPa, *Rival*: -3.81 MPa, *Corsica*: -4.24 MPa).

Table 1. Year and cultivar effect on the leaf physiological traits before defoliation. Means labeled with the same letter did not differ significantly at P<0.05. The cultivar×year interaction was not significant for any trait.

	A $\mu mol\ m^{-2}\ s^{-1}$	E $mmol\ m^{-2}\ s^{-1}$	g_s $mol\ m^{-2}\ s^{-1}$	C_i $\mu mol\ mol^{-1}$	WUE_L $\mu mol\ mmol^{-1}$	WUE_i $\mu mol\ mol^{-1}$	$Leaf\ N$ $mg\ g^{-1}$	$NO_3\text{-}N$ $mg\ kg^{-1}$	SLA $cm^2\ g^{-1}$	WP MPa	LWC $g\ g^{-1}$
Year											
2003	12.12a	6.36a	0.20a	210.4a	1.90a	62.6a	42.0a	1694a	196.4a	-4.43b	0.896a
2004	12.62a	6.71a	0.26a	203.8a	1.94a	62.7a	36.0b	2521a	99.2b	-3.47a	0.871b
Cultivar											
Europa	13.04a	7.00a	0.26a	206.9b	1.92a	58.4b	39.2a	2662a	166.4a	-3.79a	0.894a
Rival	12.19a	6.76a	0.23a	215.6a	1.81a	57.4b	37.3b	1605a	139.5b	-3.81a	0.879b
Corsica	11.94a	5.85b	0.18b	198.7c	2.03a	72.2a	40.6a	2056a	137.5b	-4.24a	0.878b

Physiological traits after re-growth

Year and sampling time affected significantly all the traits except of *A*, which showed marginally insignificant (P=0.06) differences between years (Table 2). With the exception of C_i and WUE_L, defoliation level affected significantly the physiological traits (*A*, *E*, g_s, WUE_i, leaf *N*, petiole NO_3-*N*, *SLA*, *WP*, *LWC*). Defoliation levels interacted significantly with years (*A*, g_s, leaf *N*, *WP*) and samplings (*E*, g_s). Cultivars did not differ significantly as regarded the gas exchange parameters but they showed significant differences for the other physiological traits (leaf *N*, petiole NO_3-*N*, *SLA*, *WP*, *LWC*) (Table 2).

Table 2. *ANOVA of the physiological traits determined after re-growth.*

Source	df	*A*	*E*	g_s	C_i	WUE_L	WUE_i	*Leaf N*	NO_3-*N*	*SLA*	*WP*	*LWC*
Year (Y)	1	P=0.06	***	***	***	***	***	**	***	***	*	***
Defoliation (D)	2	***	***	***	ns	ns	**	***	***	*	***	***
Y×D	2	*	ns	*	ns	ns	ns	*	ns	ns	*	ns
Cultivar (C)	2	P=0.07	ns	ns	ns	ns	ns	***	***	**	***	***
Y×C	2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
D×C	4	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
Y×D×C	4	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns
Sampling (S)	2	***	***	***	***	***	***	***	*	***	***	***
Y×S	2	**	***	***	***	***	***	***	ns	***	***	***
D×S	4	ns	*	**	ns	ns	ns	ns	ns	ns	ns	ns
Y×D×S	4	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
S×C	4	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 (%)		20.95	15.20	34.65	13.35	16.62	23.60	9.16	48.59	26.33	16.70	1.76

ns, not significant, *P<0.05, **P<0.01, ***P<0.001.

Defoliation levels increased significantly *E* and g_s but the differences among the levels were bridged with the progress of *DAD* (Figure 2). The respective trend for g_s was more pronounced in 2003 and the differences among defoliation levels were gradually eliminated with *DAD*. *SD* plants showed the highest *A* values in both years but significant differences were found only in 2003 (Figure 3). Although marginally insignificant (P=0.07), *Europa* had the highest *A* values (15.79 μmol m^{-2} s^{-1}) followed by *Rival* (15.44 μmol m^{-2} s^{-1}) and *Corsica* (14.58 μmol m^{-2} s^{-1}) (Table 3). Undefoliated plants (*C*) showed the highest WUE_i (73.32 μmol mol^{-1}), *SD* plants had the lowest values (63.88 μmol mol^{-1}) and *MD* sugar beets had moderate values (68.32 μmol mol^{-1}). Defoliation levels and cultivars affected petiole NO_3-*N*, *SLA*, *WP* and *LWC* (Table 3). The *SD* treatment showed the highest petiole NO_3-*N*, *SLA*, *WP* and *LWC*. Significant differences between *C* and *MD* plants were found only for *WP*. *Europa* and *Corsica* had the highest NO_3-*N* concentration differing significantly from *Rival*. Also, *Europa* showed the highest *SLA*, *WP* and *LWC* while the lowest values for these parameters were found in *Corsica*. Leaf *N* was highest in *SD* plants in 2004 but no significant difference between *SD* and *MD* plants was found in 2003 (Figure 4). *Corsica* had the highest leaf *N* concentration 15 and 30 *DAD*. In 40 *DAD*, *Rival* and *Corsica* had similar leaf *N* concentrations, which were significantly higher than that of *Europa* (Figure 4).
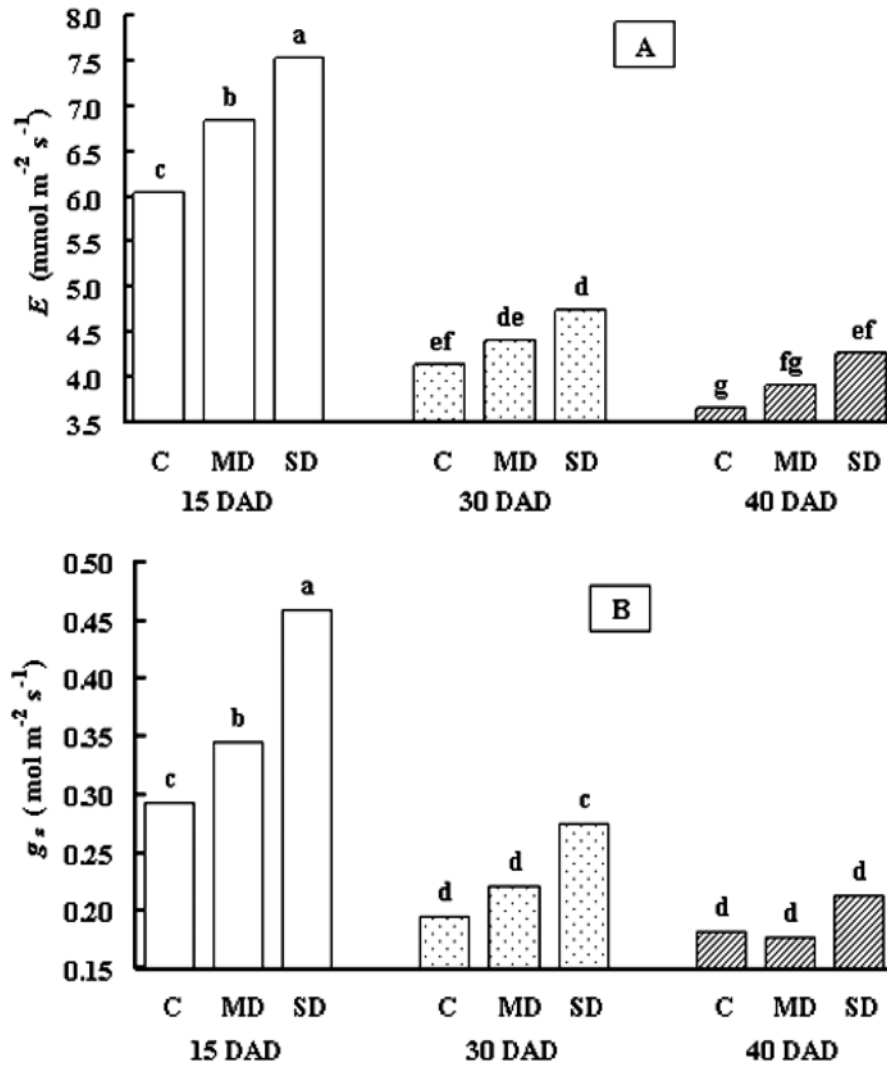
Figure 2. Transpiration rate-E, (A) and stomatal conductance-g_s (B) for the defoliation level×sampling interaction. Columns labeled with the same letter did not differ significantly at P<0.05. *DAD*: days after defoliation; *C*: control; *MD*: moderate defoliation; *SD*: severe defoliation.
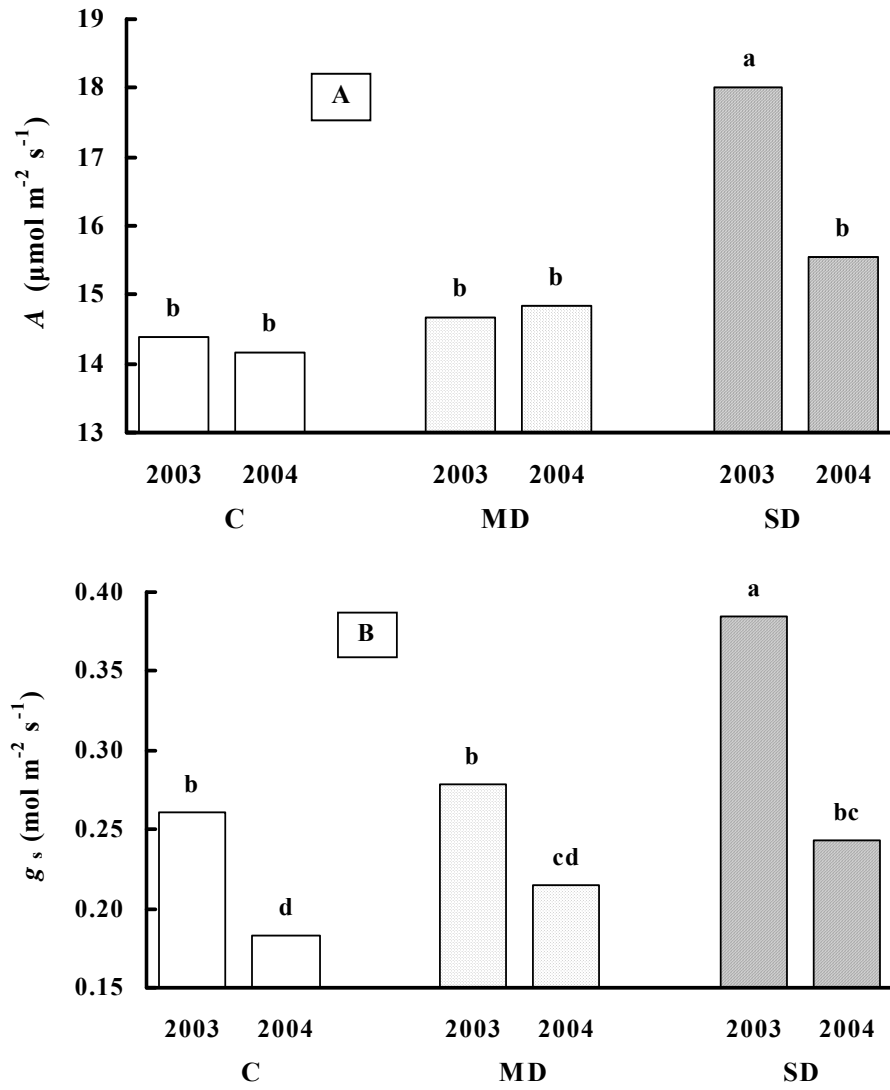
Figure 3. Net photosynthesis-*A* (A) and stomatal conductance-g_s (B) for the year×defoliation level interaction. Columns labeled with the same letter did not differ significantly at P< 0.05. *C*: control; *MD*: moderate defoliation; *SD*: severe defoliation.

Table 3. Defoliation level and cultivar effect on the leaf physiological traits after re-growth. Means labeled with the same letter did not differ significantly at P<0.05.

|	A μmol m^{-2} s^{-1}	E mmol m^{-2} s^{-1}	g_s mol m^{-2} s^{-1}	C_i μmol mol^{-1}	WUE_L μmol mmol^{-1}	WUE_i μmol mol^{-1}	$Leaf\ N$ mg g^{-1}	$NO_3\text{-}N$ mg kg^{-1}	SLA cm^2 g^{-1}	WP MPa	LWC g g^{-1}
Defoliation											
C	14.28b	4.60c	0.22b	194.8a	3.33a	73.3a	34.8b	1557b	158.0b	-2.91c	0.894b
MD	14.76b	5.04b	0.25b	195.1a	3.14a	68.3ab	36.4a	1504b	163.1ab	-2.66b	0.899b
SD	16.77a	5.50a	0.31a	197.5a	3.26a	63.9b	37.4a	2028a	176.9a	-2.22a	0.915a
Cultivar											
Europa	15.79a	5.07a	0.27a	196.4a	3.49a	68.1a	34.9b	1835a	177.4a	-2.45a	0.912a
Rival	15.44a	5.14a	0.26a	195.9a	3.54a	68.2a	35.4b	1348b	166.4ab	-2.58b	0.904b
Corsica	14.58a	4.94a	0.25a	195.1a	3.82a	69.2a	38.2a	1907a	154.3b	-2.76c	0.893b
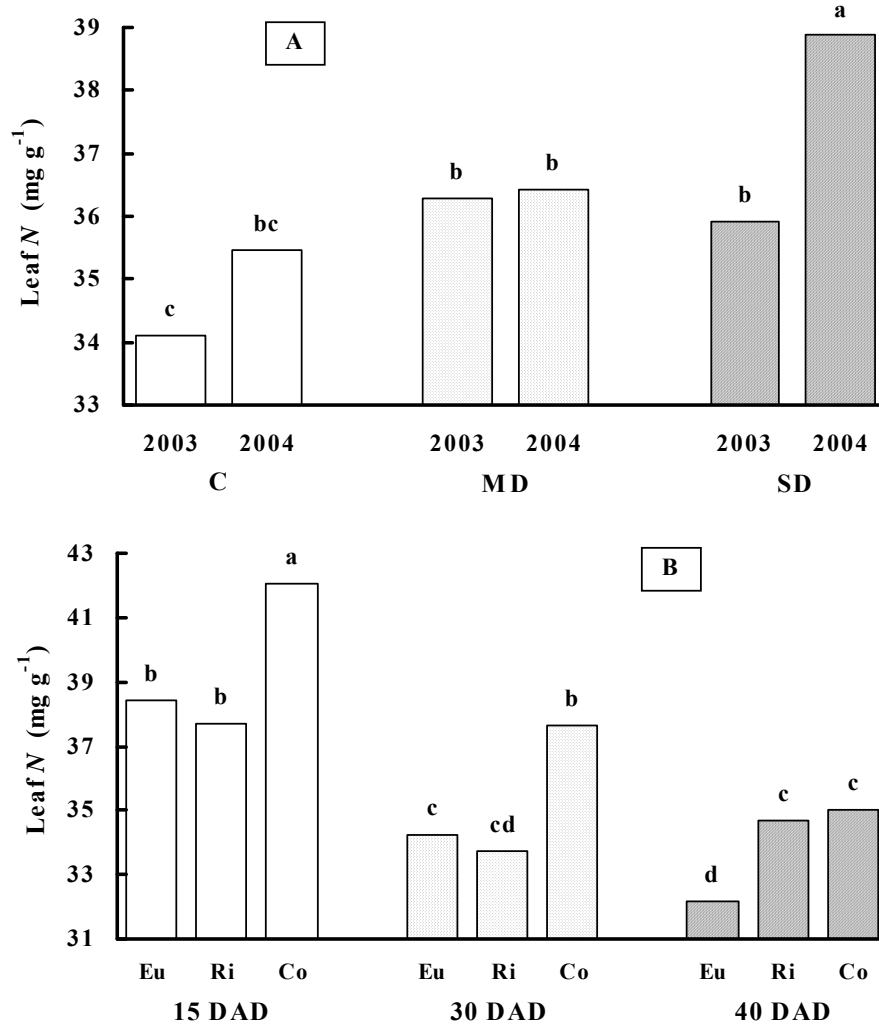
Figure 4. Leaf *N* concentration for the year×defoliation level (A) and sampling×cultivar (B) interactions. Columns labeled with the same letter did not differ significantly at P<0.05. *DAD*: days after defoliation; *C*: control; *MD*: moderate defoliation; *SD*: severe defoliation; Eu: *Europa*; Ri: *Rival*; Co: *Corsica*.

Discussion

Under the conditions of central Greece, the water shortages during July and August defoliate sugar beets; the intensity of the phenomenon depends on the severity of the abiotic conditions. However, sugar beet is considered as a well-adapted crop to water deficits in mid-or late season without any significant sugar yield reduction when irrigation is limited

to 70% of the normal (Carter et al., 1980; Winter, 1980). In central Greece, re-watering (irrigation and/or rainfall) from the beginning of August and onwards causes the rapid re-growth of sugar beets with negative effects on yield and quality. In accordance to Afanasiev (1964), Tsialtas et al. (2009) found that sugar beets can be subjected to extended defoliation (up to 75%) without significant negative effects on yield. Also, the selection of a suitable cultivar minimizes the degradation of root quality.

The compensation of yield losses in defoliated sugar beets is ascribed to that newly expanded leaves of re-grown plants are more photosynthetically active and respire less compared to intact sugar beets (French and Humphries, 1977; Carter et al., 1978).

Before defoliation

On contrary to previous reports (Bloch et al., 2006), sugar beet cultivars subjected to water stress before defoliation showed significant differences in their gas exchange physiology. Although no significant genotypic differences in long-term *WUE* (assessed by carbon isotope discrimination) have been reported previously (Tsialtas and Karadimos, 2003; Rytter, 2005), the late-season cultivar *Corsica* showed the most conservative water use (highest WUE_L) as a result of its lowest g_s. However, *Corsica* was not severely stressed since g_s was not lower than 0.10-0.15 mol m^{-2} s^{-1}, which is the value indicating severe water stress in C$_3$ species (Flexas et al., 2004). Although g_s regulates *A* in sugar beets (Kosobryukov et al., 2004; Monti et al., 2006), cultivars did not differ significantly for this parameter but they showed significant differences in their transpiration rate (*E*), which affects cultivar water economy (Mudrik et al., 2003). Although *Corsica* had the highest leaf *N* concentration, it seems that *N* was not invested in the photosynthetic machinery but in secondary compounds since it had the lowest *SLA* (Onoda et al., 2004; Tsialtas et al., 2004). Low *SLA* is considered as an adaptation of plants to water deficits (Jensen et al., 2000; Nautiyal et al., 2002). Cultivars had *LWC* close to 90%, an indication of succulence reported for Chenopodiaceae species under drought (Vendramini et al., 2002; Tsialtas et al., 2010). *LWC* is related with *SLA* and thus, with cultivar photosynthesis and water economy (Leidi et al., 1999).

After re-growth

Cultivars differed significantly only for *WP* and *LWC*; *Europa* had the highest values. These differences were not translated to differences in gas exchange physiology (*A*, *E*, g_s, C_i, WUE_L, WUE_i) among the three cultivars. The better yield and quality performance of *Corsica* compared to *Europa* and *Rival* (Tsialtas et al., 2009) should be ascribed to its better *LAI* maintenance than to the more photosynthetically active leaves of this cultivar. Based on field observations and growers' experience, *Europa* is an early-harvested cultivar since it shows high growth rates early in the growing season. This could be, probably, ascribed to its elongated tap-root, which accesses water at deep soil layers and contributes to high *WP* and *LWC* values as found here.

Sugar beets show a rapid recovery of their gas exchange physiology after re-watering (Vomáčka and Pospíšilova, 2003) but with the progress of *DAD*, a gradual decline of *A*, *E*,

g_s, and C_i was found. Adversely, water use efficiency (WUE_L, WUE_i) increased with the progress of *DAD*. The *SD* plants showed the highest *A*, *E*, g_s and leaf *N* values and MD plants followed them. However, the differences tended to be bridged with the course of *DAD*. Thus, the newly expanded leaves of re-grown sugar beets were more physiologically active and thus, increased sucrose concentration in source leaves, as a result of the higher photosynthesis. This has a positive effect on phloem loading and finally on sucrose storage in tap-roots (Winzer et al., 1996). These findings confirmed previous assumptions that higher photosynthetic rate along with lower respiration contributed to the compensation of yield losses in the defoliated sugar beets (French and Humphries, 1977; Carter et al., 1978).

The *SD* sugar beets showed a suite of traits that were indicative of their higher physiological activity. First of all, the higher photosynthetic rate (*A*) was related with the higher leaf *N* concentration (Reich et al., 1998; Tsialtas and Maslaris, 2008), which was confirmed by our findings. Sugar beet re-growth is based on both current *N* up-take and remobilization of *N* stored in roots as α-amino *N* (Pocock et al., 1990). A reliable indication of *N* nutritional status of sugar beets is the petiole NO_3-*N* (Ulrich and Hills, 1990; Oliveira et al., 1993), which was highest in *SD* plants supporting the highest leaf *N* concentration and *A* values found. Also, petiole NO_3-*N* in sugar beets is used as an osmoticum since metabolic pool is rapidly saturated (Izmailov, 2004) and thus, NO_3-*N* contributed to the highest *WP* found in *SD* plants. Confirming previous reports (Marron et al., 2003; Tsialtas et al., 2010), high *WP* was related with high *LWC* and *SLA*. Higher *SLA* is indicative of thinner leaves, shorter leaf life span and higher *RGR* (Castro-Díez et al., 2000; Wright and Westoby, 2001; Vendramini et al., 2002).

Conclusions

Before defoliation when cultivars were subjected to water stress, the late-season cultivar *Corsica* showed the most conservative water use (highest WUE_i) due to its lowest *E* and g_s. After the re-watering and the subsequent re-growth, cultivars differed only for *WP* and *LWC* with the early-harvested cultivar *Europa* to have the highest values. Thus, the good yield and quality performance of *Corsica* after re-growth, as reported by Tsialtas et al. (2009), should be ascribed to its better *LAI* maintenance than to its leaf physiological superiority compared to *Europa* and *Rival*. The *SD* plants were the most physiologically active showing the highest *A*, *E*, g_s and leaf *N* concentration. This finding accompanied by the assumption that the newly expanded leaves respire less could be the mechanism by which defoliated sugar beets compensate for yield and quality losses (Tsialtas et al., 2009).

Acknowledgements

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