Leaf physiological traits and its relation with sugar beet cultivar success in two contrasting environments

J.T. Tsialtas[a,*], N. Maslaris[b]

[a]*Aristotle University of Thessaloniki, School of Agriculture, Laboratory of Agronomy, 541 24 Thessaloniki, Hellas.*
[b]*Hellenic Sugar Industry SA, Agronomic Research Service, 574 00 Sindos, Hellas.*
*Corresponding author. E-mail: tsialtas01@windowslive.com

Abstract

The aim of this study was to identify leaf physiological traits, which could be used in selecting high yielding genotypes among 12 sugar beet cultivars grown in two contrasting pedo-climatic environments. In the stressful Site 1 (high temperatures, low rainfall, heavy-textured soil), high yielders had cooler leaves (lower ΔT) and thus, transpired (E) and photosynthesized (A) more. Also, these cultivars had higher chlorophyll content, as assessed by *SPAD* readings, supporting that staying green under stress conditions contributes to final yield. On the contrary, in the favorable Site 2 (mild temperatures, high rainfall, light-textured soil), high yielding cultivars had higher leaf area index ($LAI > 3.5$-4.0). In Site 2, a negative correlation between *SPAD* and yields (fresh root weight-*FRW* and sugar yield-*SY*) indicated that the investment in high leaf greenness under favorable conditions is a disadvantage for sugar beet productivity. Combining data of both sites, the optimum values of physiological traits related to yields (*FRW* and *SY*) were estimated, respectively, at -0.59 to -053 ºC for ΔT, 20.37 to 19.26 μmol m^{-2} s^{-1} for A and 8.97 to 8.86 mmol m^{-2}s^{-1} for E. It is proposed the use of *SPAD* as an easy, rapid and non-destructive screening for sugar beet high yielders under both stressful and favorable growing conditions.

Keywords: *Beta vulgaris* L.; Photosynthesis; *SPAD*; Sugar yield.

Abbreviations

A: net photosynthesis; *ANOVA*: analysis of variance; C_i: intracellular CO_2 concentration; ΔT: T_l-T_a; E: transpiration rate; *FRW*: fresh root weight;

$G{\times}E$: genotype×environment; g_s: stomatal conductance; *LA*: leaf area; *LAI*: leaf area index; *LSD*: least significant difference; *RCB*: Randomized Complete Block; *RGR*: relative growth rate; *SC*: % sucrose content in fresh root weight; *SLA*: specific leaf area; *SPAD*: soil-plant analysis development; *SY*: sugar yield; T_a: air temperature; T_l: leaf temperature; *WUE*: water use efficiency.

Introduction

Sugar beets (*Beta vulgaris* L.) are grown on various soils and under different climatic conditions worldwide. Location and year are considered as the main factors affecting sugar beet productivity and they account for over 80% of yield variability (Märländer et al., 2003; Hoffmann et al., 2009).

In Greece, sugar beets grow as a spring crop in central and northern country, which has a fragmented terrain and thus, shows many pedo-climatic micro-environments. The yield formation in sugar beet is affected by such conditions and the genotype × environment (G×E) interactions are strong (Tsialtas and Maslaris, 2009). However, the study of sugar beet physiological response at various environments especially at leaf level and under field conditions is limited. Only recently, researchers began to work on the physiological responses of sugar beet genotypes to abiotic stresses such as drought (Ober et al., 2005; Pidgeon et al., 2006; Luković et al., 2009). The decoding of the relationship between physiological traits and yield could be beneficial for sugar beet improvement since physiological traits could be used as indirect criteria for increased selection accuracy (Edmeades et al., 2004; Ober et al., 2005).

Ober et al. (2005) found that greenness index, a measure of green color intensity of the leaves, can be used as a selection criterion for drought tolerant genotypes. Actually, these researchers made an assessment of the chlorophyll content at canopy level. An easy, rapid and non-destructive method for the assessment of leaf chlorophyll concentration is the use of *SPAD*-502 meter, as it was proven for many species (Kapotis et al., 2003; Murillo-Amador et al., 2004; Wang et al., 2004; Martin et al., 2007), sugar beet included (Malnou et al., 2008). *SPAD* readings are a good indicator of yield and quality in crops such as winter wheat, rice, spinach and peanuts (Ramesh et al., 2002; Le Bail et al., 2005; Liu et al., 2006; Songsri et al.,

2008). In sugar beet cultivars, although seasonal changes were revealed, no relationship between yield and *SPAD* was found (Pulkrábek et al., 2001).

SPAD readings have been proved to be a high heritable trait (Nigam and Aruna, 2008; Songsri et al., 2008) that it could be used to identify genotypes with good photosynthetic machinery (Giunta et al., 2002). Improvements in the rate of photosynthesis have contributed to yield increases in crops like wheat (Jiang et al., 2003) and there is potential for further increases in both photosynthesis and yield (Long et al., 2006). However, it has been reported that high photosynthetic rate is an advantage for genotype success in resource non-limiting environments while in stressful environments; traits relating to persistence could be beneficial (Arntz et al., 2000). Environment can affect photosynthesis significantly and in sugar beets, reductions higher than 15% have been reported from temperate to Mediterranean environments (Vandendriessche et al., 1990; Tsialtas and Maslaris, 2008a). In C_3 species, sugar beet included, the photosynthetic rate is strongly regulated by the stomatal functioning meaning that factors (e.g. drought), which cause stomata closure, decrease CO_2 assimilation (Cornic, 2000; Flexas and Medrano, 2002; Monti et al., 2006; Tsialtas and Maslaris, 2008a). As a result of stomata closure, leaf transpiration is reduced (Matsumoto et al., 2005), leaf temperature and concurrently canopy temperature increase (Blum et al., 1989; Rashid et al., 1999) thus, crop productivity is limited by the lower crop evapotranspiration (Davidoff and Hanks, 1989; Jaggard et al., 2009).

The rapid formation of a leaf area index (*LAI*) higher than 3.5-4.0 is necessary for maximizing (> 85%) solar radiation interception (Jaggard and Qi, 2006; Tsialtas and Maslaris, 2008b), which along with the maintenance of an adequate *LAI* for as long as possible during the growing season contribute to crop productivity (Liu et al., 2005; Cerkal et al., 2007). Specific leaf area (*SLA*, the ratio of dry leaf mass per leaf surface unit) is a physiological parameter related with plant resource-use strategy (Wilson et al., 1999; Vendramini et al., 2002), leaf morphology, leaf life span and relative growth rate (*RGR*) (Castro-Díez et al., 2000; Wright and Westoby, 2001). Recently, it has been reported (Rajabi et al., 2008; Tsialtas et al., 2010) that *SLA* is related with sugar beet water use efficiency (*WUE*) as it was assessed by carbon isotope discrimination (*Δ*, a measure of the $^{13}C/^{12}C$ ratio in plant tissues compared to the air).

Concluding, physiological traits could explain genotypic response to different environments and could be useful tools for selecting the most productive genotypes in each specific environment. However, field works studying the variation of leaf physiological traits of sugar beet genotypes and relating them to yield and quality are limited. Thus, the aim of this work was to study the variation of leaf physiological traits (ΔT, A, g_s, E, C_i, A/E, A/g_s, *SPAD*, *LAI*, *SLA*, *LA*) in 12 sugar beet cultivars grown in two contrasting environments of central Greece and to relate them with yield (*FRW*, *SY*) and root quality (*SC*, *K*, *Na*, *α-amino N* in roots).

Materials and Methods

The experimentation took place during 2002 growing season in two sites in central Greece, which have contrasting pedo-climating characteristics. Amfithea (Site 1) is located in eastern Thessaly Plain (39º 43' 1N, 22º 28' 1E, 76 m elevation), on a heavy inorganic soil, with typical Mediterranean climate (Table 1). Pyrgetos (Site 2) is a littoral site (39º 55' 0N, 22º 37' 3E, 25 m elevation), on a light-textured soil, with a milder climate (Table 1). Site 1 is a rhizomania-prone and Site 2 is a cercospora-prone location, respectively.

Twelve rhizomania-tolerant sugar beet cultivars, obtained from five breeders (*Hellenic Sugar Industry SA*, Thessaloniki, Greece, *SESVANDERHAVE NV/SA*, Tienen, Belgium, *Maribo Seed International ApS*, Holeby, Denmark, *KWS SAAT AG*, Einbeck, Germany and *Hilleshög-Syngenta Seeds AB*, Landskrona, Sweden), were mechanically drilled (Site 1: 1 April, Site 2: 24 April) in four rows (8 m long) per plot, at 50 cm apart and at 10 cm spacing in the row. The experiments were arranged in Randomised Complete Block (*RCB*) design with six replications. At the two-true leaf stage, seedlings were thinned by hand in order to establish a theoretical population of 100000 plants ha^{-1}. Fertilization was applied as both basal (55 kg N ha^{-1}, 75 kg P$_2$O$_5$ ha^{-1}, 75 kg K$_2$O ha^{-1}) and top-dressing (103.5 kg N ha^{-1}) before canopy closure. Supplemental irrigation was provided at both sites (Site 1: 250 mm and Site 2: 135 mm). Weeds were suppressed by hand-weeding and chemical spraying. Full protection was taken against cercospora leaf spot, powdery mildew and insects by sprayings.

Table 1. Pedo-climatic characteristics of the two experimental sites.

	Soil analysis			pH	CaCO₃	Org. C	NO₃-N	P-Olsen	Exchangable cations		Climatic parameters*	
	Sand	Silt	Clay						K	Na	Temperature	Rainfall
	%			1:1	%			mg kg⁻¹			°C	mm
Amfithea	15	23	62	8.2	0.5	1.03	5.3	8.2	190	146	19.3	343
Pyrgetos	39	39	22	8.2	3.5	0.87	7.2	8.3	68	41	18.8	513

*The mean temperature and the total rainfall during the growing season (March to October) are given.

Leaf physiological measurements were conducted at early July when *LAI* reaches its maximum under the Greek conditions. *LAI* was determined using *SunScan* canopy analysis system (*Delta-T Devices Ltd*, Cambridge, UK). Two measurements were taken between the 2nd and the 3rd rows in each plot and the average was calculated. Leaf chlorophyll content was assessed using *SPAD*-502 (*Minolta Co Ltd*, Osaka, Japan) on 10 full-expanded, intact and full sun-lit leaves per plot. The measurements were taken adaxially, at the right side and on the middle of the leaf. The average value of the 10 measurements was the *SPAD* reading of each plot. Gas exchange measurements (net photosynthesis-*A*, transpiration rate-*E*, stomatal conductance-g_s, intracellular CO_2 concentration-C_i) were conducted in three upper, full-expanded, intact, and full sun-lit leaves using LC_i portable photosynthesis system (*ADC BioScientific Ltd*, Hoddesdon, UK). Instantaneous water use efficiency and photosynthetic water use efficiency were estimated as *A/E* and A/g_s ratios, respectively. All determinations took place at midday (11.00 h to 13.00 h). Three leaves, similar to those used for gas exchange measurements, were collected per plot, put on ice-chest and transferred to the Crop Physiology Lab of Larissa factory, Hellenic Sugar Industry SA. They were used for leaf area (*LA*) measurements using *WinDias* image analysis system (*Delta-T Devices Ltd*, Cambridge, UK). After drying at 75 °C for 48 h, specific leaf area (*SLA*, cm^2 g^{-1}) was estimated as the ratio of *LA* to dry weight.

Harvest took place on 5 November at Site 1 and on 24 October at Site 2. The two internal rows (2nd and 3rd) were harvested by hand at a length of 7 m (7 m^2) per plot. Sugar beets were topped by hand, root number was counted and fresh root weights (*FRW*) were measured. A randomly selected root sub-sample (25-30 roots), from each plot, was transferred to factory's tare house for qualitative determinations *(% sucrose content in fresh root, K, Na, α-amino N concentration)*. Root quality was determined using *Venema* automatic beet laboratory system (*Venema automation b.v.*, Groningen, Holland) connected with a *BETALYSER*® analyzing system (*Dr Wolfgang Kernchen GmbH*, Seelze, Germany).

The data were subjected to *ANOVA* as *RCB* design with six replications and with sites and cultivars as main factors. The analysis was conducted using *MSTAT-C* (version *1.41*, Crop and Soil Sciences Department, Michigan State University, USA) and the means were compared with *LSD* test.

Results

Yield and root quality

ANOVA revealed that the main factors (sites and cultivars) and their interaction had significant effects on quantitative (*FRW*, *SY*) and qualitative (*SC*, *K*, *Na*, *α-amino N* in roots) traits. Cultivars affected all the determined traits, sites did not affect *SY* and *Na* concentration in roots and the interaction was not significant only for *α-amino N* concentration.

FRW was higher in Site 2 (99.9 t ha^{-1}) compared to Site 1 (90.1 t ha^{-1}). The highest *FRW* was recorded for cv. *Ramona* in Site 2 (111.0 t ha^{-1}) and the lowest for cv. *Turbo* in Site 1 (62.6 t ha^{-1}) (Table 2). Adversely to *FRW*, the *SC* was higher in Site 1 (14.3%) compared to Site 2 (12.9%). In the former site, the *SC* ranged from 13.4% (*Europa*) up to 15.3% (*Visa*) and in the latter site, from 11.8% (*Europa*) up to 13.6% (*Turbo*) (Table 2). *SY* was similar in both sites (12.8 and 12.9 t ha^{-1}, respectively) but it was more variable in Site 1 (ranged from 8.5 up to 15.1 t ha^{-1}) compared to Site 2 (ranged from 10.9 up to 13.6 t ha^{-1}) (Table 2).

Potassium concentration in roots was highest in Site 2 (1101 and 1514 mg 100g^{-1} sucrose, respectively). In Site 1, *Impact* had the lowest *K* concentration (984 mg 100g^{-1} sucrose) and *Europa* the highest one (1258 mg 100g^{-1} sucrose). In Site 2, the respective values were recorded for *Ramona* and *Ariete* (1653 and 1358 mg 100g^{-1} sucrose, respectively). In both sites, *Na* concentrations in roots were high. In Site 1, *Europa* had the highest *Na* concentration (522.2 mg 100g^{-1} sucrose) and *Electra*, the lowest one (302 mg 100g^{-1} sucrose). The respective values in Site 2 were recorded for *Europa* (542.1 mg 100g^{-1} sucrose) and *Bianca* (319.4 mg 100 g^{-1} sucrose). The concentration of *α-amino N* in Site 2 was 2.5-fold higher than that in Site 1 (142.6 and 359.3 mg 100g^{-1} sucrose, respectively). In the latter site, harmful *N* ranged from 122.1 mg 100g^{-1} sucrose (*Impact*) up to 177.1 mg 100g^{-1} sucrose (*Bianca*). In Site 2, *Rizor* had the highest (412.2 mg 100g^{-1} sucrose) and *Ariete* the lowest *α-amino N* concentration in roots (322.6 mg 100g^{-1} sucrose).

Table 2. Fresh root weight (*FRW*), % sucrose content in fresh root weight (*SC*), sugar yield (*SY*) and root impurities (*K*, *Na*, *α-amino N*) for the 12 cultivars in the two sites. Each mean is the average of six replications.

Cultivar	FRW (t ha⁻¹)		SC (%)		SY (t ha⁻¹)		K (mg 100 g⁻¹ sucrose)		Na (mg 100 g⁻¹ sucrose)		α-amino N (mg 100 g⁻¹ sucrose)	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Fresno	101.8[a-f]	103.7[a-d]	14.8[ab]	13.0[i-l]	15.1[ab]	13.4[c-e]	1082[g-j]	1470[b-d]	381.7[d-h]	438.4[a-f]	140.3[ef]	352.7[b-d]
Turbo	62.6[k]	94.0[d-h]	13.6[e-i]	13.6[c-i]	8.5[i]	12.8[de]	1213[fg]	1435[cd]	439.1[a-f]	341.8[f-h]	131.5[f]	342.6[cd]
Electra	88.0[hi]	94.4[d-h]	14.8[a-c]	13.0[i-l]	13.0[de]	12.2[e-g]	1125[f-i]	1593[ab]	302.0[h]	355.0[f-h]	161.0[ef]	387.0[ab]
Bianca	76.7[j]	93.4[c-h]	13.9[d-h]	13.2[h-k]	10.6[h]	12.3[e-g]	1089[g-j]	1487[b-d]	485.5[a-e]	319.4[gh]	177.1[e]	343.6[cd]
Ramona	88.7[g-i]	111.0[a]	14.3[b-e]	12.3[lm]	12.7[d-f]	13.6[b-e]	1109[g-j]	1653[a]	372.4[c-h]	436.1[a-f]	147.0[ef]	383.9[a-c]
Dorothea	102.9[a-e]	104.2[a-c]	14.8[a-c]	12.7[kl]	15.2[a]	13.2[c-e]	1061[h-j]	1567[a-c]	376.9[e-h]	423.7[b-g]	158.6[ef]	350.4[b-d]
Doria	101.0[b-f]	109.6[ab]	14.0[d-g]	12.3[lm]	14.1[a-d]	13.5[c-e]	1130[f-i]	1628[a]	497.7[a-c]	454.1[a-f]	131.6[f]	348.0[b-d]
Rizor	79.6[ij]	95.1[c-h]	14.1[c-f]	12.9[j-l]	11.2[f-h]	12.3[e-g]	1163[f-h]	1585[ab]	493.4[a-d]	387.5[c-h]	139.3[ef]	412.2[a]
Impact	98.3[c-g]	99.6[c-f]	14.7[a-c]	12.7[kl]	14.5[a-c]	12.6[d-f]	984[j]	1578[ab]	362.8[f-h]	443.8[a-f]	122.1[f]	349.3[b-d]
Ariete	92.3[f-h]	103.7[a-d]	14.4[b-d]	13.2[h-k]	13.3[c-e]	13.6[b-e]	1000[ij]	1358[de]	387.3[c-h]	388.0[c-h]	134.6[ef]	322.6[d]
Visa	86.3[h-j]	97.8[c-g]	15.3[a]	13.5[f-j]	13.2[c-e]	13.1[c-e]	1003[ij]	1382[de]	305.0[h]	383.0[c-h]	125.3[f]	323.0[d]
Europa	103.7[a-d]	92.2[f-h]	13.4[g-j]	11.8[m]	13.9[a-d]	10.9[gh]	1258[ef]	1435[cd]	522.2[ab]	542.1[a]	143.0[ef]	395.8[a]
	90.1	99.9	14.3	12.8	12.9	12.8	1101	1514	410.5	409.4	142.6	359.3

For the same column, means labeled with the same letter did not differ significantly at P<0.05. The average value for each site is given at the end of each column.

Leaf physiological traits

Sites affected all the determined traits whereas cultivars had a significant effect only on *SPAD* and *A/E*. The interaction of the main factors (sites×cultivars) was not significant for any trait.

ΔT was highest in Site 1 (-0.371 and -0.613 ºC, respectively) and *Turbo* had the highest value (-0.196 ºC). *Bianca* had the lowest ΔT (-0.777 ºC) in Site 2 (Table 3). Net photosynthesis (*A*) was higher in Site 2 (21.00 µmol m^{-2} s^{-1}) compared to Site 1 (17.34 µmol m^{-2} s^{-1}) with *Europa* having the highest (18.98 and 22.59 µmol m^{-2} s^{-1}, respectively) and *Turbo* the lowest (15.44 and 19.84 µmol m^{-2} s^{-1}, respectively) values in both sites (Table 3). Transpiration rate (*E*) was highest in Site 2 (8.47 and 8.86 mmol m^{-2} s^{-1}, respectively). The lowest *E* was recorded for *Rizor* in Site 1 (7.90 mmol m^{-2} s^{-1}) and the highest for *Visa* in Site 2 (9.34 mmol m^{-2} s^{-1}) (Table 3). Site 2 had a 4-fold higher g_s compared to Site 1 (0.52 and 2.05 mol m^{-2} s^{-1}, respectively). In Site 1, the values ranged from 0.41 mol m^{-2} s^{-1} (*Rizor*) to 0.57 mol m^{-2} s^{-1} (*Ramona, Impact*) whereas in Site 2, the lowest value was 1.41 mol m^{-2} s^{-1} (*Ariete*) and the highest 2.68 mol m^{-2} s^{-1} (*Rizor*). Intracellular CO_2 concentration (C_i) was 241.1 µmol mol^{-1} in Site 2 and 224.3 µmol mol^{-1} in Site 1. The lowest C_i was recorded for *Rizor* in Site 1 (218.8 µmol mol^{-1}) and the highest for *Ariete* in Site 2 (249.0 µmol mol^{-1}). *Impact* had the lowest (1.861 µmol mmol^{-1}) and *Visa* had the highest (2.240 µmol mmol^{-1}) *A/E* values in Site 1. The respective values in Site 2 were found for *Impact* and *Electra* (2.189 and 2.561 µmol mmol^{-1}, respectively). A 3-fold higher A/g_s was recorded in Site 1 (36.95 µmol mol^{-1}) compared to Site 2 (12.20 µmol mol^{-1}) (Table 3). *Fresno* had the highest A/g_s in both sites (41.03 and 14.76 µmol mol^{-1}, respectively). The lowest values were recorded for *Visa* in Site 1 (32.42 µmol mol^{-1}) and *Bianca* in Site 2 (9.35 µmol mol^{-1}).

SPAD was higher in Site 2 (44.8 units) compared to Site 1 (42.4 units). (Table 4). *Europa* had the highest *SPAD* readings in both sites (45.9 and 48.3 units, respectively). The lowest *SPAD* was recorded for *Bianca* in Site 1 (39.5 units) and *Doria* in Site 2 (41.4 units). *Ramona* had the lowest *LAI* (1.78 m^2 m^{-2}) in Site 1 and *Europa* (3.14 m^2 m^{-2}) in Site 2 (Table 4). The highest values were recorded for *Visa* in Site 1 and *Dorothea* in Site 2 (2.72 and 5.03 m^2 m^{-2}, respectively). *LA* was higher in Site 2 (355.7 cm^2) compared to Site 1 (230.6 cm^2) (Table 4). In the latter site, *LA* ranged from 219.1 cm^2 (*Impact*) to 240.4 cm^2 (*Electra*). In Site 2, the highest *LA* was recorded for *Fresno* (389.0 cm^2) and the lowest for *Europa* (328.0 cm^2). *SLA* was highest in Site 1 (152.7 and 140.7 cm^2 g^{-1}, respectively). In Site 1, *Turbo* and *Electra* had the highest and the lowest values (162.1 and 136.7 cm^2 g^{-1}, respectively). *Ariete* and *Visa* had the respective values (156.2 and 123.4 cm^2 g^{-1}) in Site 2 (Table 4).

Table 3. Gas exchange and related traits for the 12 cultivars in the two sites. Each mean is the average of six replications.

Cultivar	(°C)		A (µmol m⁻² s⁻¹)		E (mmol m⁻² s⁻¹)		g_s (mol m⁻² s⁻¹)		C_i (µmol mol⁻¹)		A/E (µmol mmol⁻¹)		A/g_s (µmol mol⁻¹)	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Fresno	-0.367[a-d]	-0.643[c-e]	18.25[c-k]	21.28[ab]	8.64[ab]	8.71[ab]	0.47[d]	1.88[bc]	228.6[d-j]	235.2[a-i]	2.118[c-i]	2.486[ab]	41.03[a]	14.76[c]
Turbo	-0.196[a]	-0.473[a-e]	15.44[k]	19.84[a-h]	8.09[ab]	8.63[ab]	0.54[d]	1.87[bc]	228.3[c-j]	239.5[a-f]	1.881[hi]	2.325[a-e]	33.96[ab]	13.69[c]
Electra	-0.360[a-d]	-0.403[a-e]	17.71[e-k]	21.27[ab]	8.59[ab]	8.38[ab]	0.53[d]	1.75[bc]	219.2[ij]	232.4[b-j]	2.068[d-i]	2.561[a]	34.43[ab]	14.55[c]
Bianca	-0.360[a-d]	-0.777[e]	16.95[h-k]	20.04[a-g]	8.24[ab]	8.91[ab]	0.52[d]	2.27[ab]	228.2[c-j]	248.3[ab]	2.048[d-i]	2.252[a-g]	36.90[ab]	9.35[c]
Ramona	-0.423[a-e]	-0.553[a-e]	17.00[h-k]	22.20[a]	8.39[ab]	8.76[ab]	0.57[d]	2.42[ab]	227.6[c-j]	237.2[a-g]	2.017[e-i]	2.546[a]	35.63[ab]	10.09[c]
Dorothea	-0.467[a-e]	-0.570[a-e]	17.76[d-k]	20.56[a-e]	8.96[ab]	8.50[ab]	0.50[d]	1.95[a-c]	220.1[h-j]	243.0[a-e]	1.978[g-i]	2.425[a-c]	38.21[ab]	13.04[c]
Doria	-0.350[a-d]	-0.653[c-e]	17.18[g-k]	20.68[a-d]	8.63[ab]	8.88[ab]	0.53[d]	1.83[bc]	220.9[h-j]	239.2[a-f]	1.983[f-i]	2.351[a-d]	38.59[ab]	11.71[c]
Rizor	-0.250[ab]	-0.694[de]	15.98[jk]	21.18[a-c]	7.90[b]	9.18[a]	0.41[d]	2.68[a]	218.8[j]	244.5[a-d]	2.027[d-i]	2.306[a-f]	40.51[ab]	10.03[c]
Impact	-0.470[a-e]	-0.713[de]	16.71[i-k]	20.37[a-f]	8.88[ab]	9.30[a]	0.57[d]	2.28[ab]	225.9[f-j]	246.1[a-c]	1.861[i]	2.189[b-h]	32.84[ab]	10.05[c]
Ariete	-0.303[a-c]	-0.685[c-e]	17.51[f-k]	20.54[a-e]	8.23[ab]	8.85[ab]	0.46[d]	1.41[c]	222.5[g-j]	249.0[a]	2.089[d-i]	2.344[a-d]	40.79[ab]	16.72[c]
Visa	-0.443[a-e]	-0.627[b-e]	18.66[b-j]	21.45[ab]	8.44[ab]	9.34[a]	0.62[d]	2.29[ab]	230.2[c-j]	242.8[a-e]	2.240[a-g]	2.290[a-g]	32.42[b]	11.47[c]
Europa	-0.460[a-e]	-0.558[a-e]	18.98[b-i]	22.59[a]	8.71[ab]	8.88[ab]	0.56[d]	2.10[a-c]	220.9[h-j]	235.9[a-h]	2.163[b-i]	2.553[a]	38.08[ab]	10.91[c]
	-0.371	-0.613	17.34	21.00	8.47	8.86	0.52	2.05	224.3	241.1	2.039	2.386	36.95	12.20

For the same column, means labeled with the same letter did not differ significantly at P<0.05. The average value for each site is given at the end of each column.

Table 4. *SPAD*, *LAI*, *LA* and *SLA* values for the 12 cultivars in the two sites. Each mean is the average of six replications.

Cultivar	SPAD (units)		LAI ($m^2 m^{-2}$)		LA (cm^2)		SLA ($cm^2 g^{-1}$)	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Fresno	45.2[a-d]	44.0[b-e]	2.07[ij]	4.18[a-d]	229.7[c]	389.0[a]	149.1[a-d]	155.8[a-c]
Turbo	39.6[f]	44.9[a-d]	2.13[ij]	4.15[a-d]	236.6[c]	369.4[ab]	162.1[a]	130.4[de]
Electra	43.4[b-f]	45.8[a-c]	2.57[f-j]	3.50[c-h]	240.4[c]	350.8[ab]	136.7[b-e]	152.7[a-d]
Bianca	39.5[f]	45.2[a-d]	2.40[g-j]	4.82[ab]	227.2[c]	388.9[a]	153.9[a-d]	147.2[a-e]
Ramona	42.5[c-f]	46.6[ab]	1.78[j]	4.53[a-c]	231.0[c]	342.4[b]	145.5[a-e]	142.1[a-e]
Dorothea	44.0[b-e]	43.8[b-e]	2.70[e-j]	5.03[a]	232.4[c]	328.6[b]	156.0[a-c]	130.0[d-e]
Doria	42.3[c-f]	41.4[d-f]	2.38[g-j]	4.93[a]	227.6[c]	368.6[ab]	151.3[a-d]	142.2[a-e]
Rizor	42.2[c-f]	45.8[a-c]	2.65[e-j]	3.62[b-g]	236.2[c]	347.8[ab]	147.2[a-e]	141.8[a-e]
Impact	42.6[c-f]	44.1[b-e]	2.32[h-j]	3.82[a-f]	219.1[c]	351.3[ab]	161.3[ab]	136.5[c-e]
Ariete	40.9[ef]	43.6[b-e]	2.40[g-j]	3.92[a-e]	230.2[c]	350.7[ab]	157.0[a-c]	156.2[a-c]
Visa	40.5[ef]	44.0[b-e]	2.72[e-j]	4.20[a-d]	236.3[c]	352.4[ab]	152.3[a-d]	123.4[e]
Europa	45.9[a-c]	48.3[a]	2.22[ij]	3.14[d-i]	220.7[c]	328.0[b]	159.7[a-c]	130.4[de]
	42.4	44.8	2.36	4.15	230.6	355.7	152.7	140.7

For the same column, means labeled with the same letter did not differ significantly at $P<0.05$. The average value for each site is given at the end of each column.

Correlations between physiological traits

ΔT was negatively correlated with *A* and *E* in Site 1 (r=-0.69, P<0.05, n=12 and r= -0.81, P<0.01, n=12, respectively). In Site 2, weak or moderate, negative correlations related ΔT with *E* and C_i (r= -0.67, P<0.05 and r=-0.77, P<0.01, n=12, respectively). Combining the data of both sites, ΔT was negatively correlated to the physiological traits with the exception of *A/E* and *SLA* (Table 5). In Site 2, *A-SPAD* and g_s-*E* were positively correlated (r= 0.61 and r= 0.60, respectively, P<0.05, n=12) whereas *SPAD* and *LAI* gave a significant, negative correlation (r=-0.60, P<0.05, n=12).

Significant correlations were found when the data of both sites were combined (Table 5). However, the significance of these correlations was driven by the site effect on the determined traits and not by a genotypic effect.

Table 5. Correlation coefficients and significance level of the interrelationships of the physiological traits. n=12 for Site 1 and Site 2 and n=24 for Total (Site 1 and Site 2).

		A	E	g_s	C_i	A/E	A/g_s	SPAD	LAI	LA	SLA
	Site 1	-0.69*	-0.81**	ns	ns	ns	ns	ns	ns	ns	ns
ΔT	*Site 2*	ns	-0.67*	ns	-0.77**	ns	ns	ns	ns	ns	ns
	Total	-0.77***	-0.81***	-0.81***	-0.84***	ns	0.81***	-0.48*	-0.76***	-0.79***	ns
	Site 1		ns	ns	ns	0.79**	ns	ns	ns	ns	ns
A	*Site 2*		ns	ns	ns	0.61*	ns	0.61*	ns	ns	ns
	Total		0.62**	0.88***	0.73***	ns	-0.88***	0.71***	0.76***	0.84***	-0.54**
	Site 1			ns	ns	ns	ns	0.64*	ns	ns	ns
E	*Site 2*			0.60*	ns	ns	ns	ns	ns	ns	ns
	Total			0.63***	0.57**	ns	-0.59**	0.52**	0.46*	0.52**	ns
	Site 1				ns	ns	-0.83***	ns	ns	ns	ns
g_s	*Site 2*				ns	ns	-0.87***	ns	ns	ns	ns
	Total				0.86***	ns	-0.97***	0.58**	0.85***	0.93***	-0.61**
	Site 1					ns	ns	ns	ns	ns	ns
C_i	*Site 2*					ns	ns	ns	ns	ns	ns
	Total					ns	-0.89***	ns	0.80**	0.86***	0.47*
	Site 1						ns	ns	ns	ns	ns
A/E	*Site 2*						ns	ns	ns	ns	ns
	Total						ns	ns	ns	ns	ns
	Site 1							ns	ns	ns	ns
A/g_s	*Site 2*							ns	ns	ns	ns
	Total							-0.52**	-0.88***	-0.95***	0.57**
	Site 1								ns	ns	ns
SPAD	*Site 2*								-0.60*	ns	ns
	Total								ns	0.48*	-0.41*
	Site 1									ns	ns
LAI	*Site 2*									ns	ns
	Total									0.91***	0.52**
	Site 1										ns
LA	*Site 2*										ns
	Total										-0.49*

ns: not significant; *, **, ***: significance at P<0.05, P<0.01, P<0.001, respectively.

Relationships of the physiological traits with yield (FRW, SY) and quality (SC, K, Na, α-amino N)

Yields (*FRW*, *SY*) were positively correlated with *ΔT* in Site 1 (r= 0.72 and r= 0.74, respectively, P<0.01, n=12) but no significant correlation was evident in Site 2 (Figure 1). Combining data of both sites, quadratic functions were the best-fitted curves for both *FRW* and *SY* with the *ΔT-FRW* relationship to be the stronger (r^2= 0.60, P<0.001 and r^2= 0.38, P<0.01, respectively). From the first derivative (linear function) of the quadratic

functions (*ΔT-FRW* and *ΔT-SY*), the optimum *ΔT* for maximum yield was estimated at -0.59 °C and -0.53 °C for *FRW* and *SY*, respectively.

In Site 1, both *A* and *E* were linearly and positively related to yields (*FRW*, *SY*) with correlations being stronger for *E* (Figure 2). In combined data, yields were curvilinearly related to both physiological traits. The quadratic functions were stronger for *FRW* compared to *SY* (Figure 2). The optimum *A* values for maximum yield were estimated at 20.37 μmol m^{-2} s^{-1} and 19.26 μmol m^{-2} s^{-1} for *FRW* and *SY*, respectively. Regarding *E*, the optimum values were found to be 8.97 mmol m^{-2} s^{-1} and 8.86 mmol m^{-2} s^{-1} for *FRW* and *SY*, respectively. In Site 2, a negative correlation between *A* and *SC* was evident (*SC*= -0.4088*A* + 21.409, r= -0.65, P<0.05, n=12).
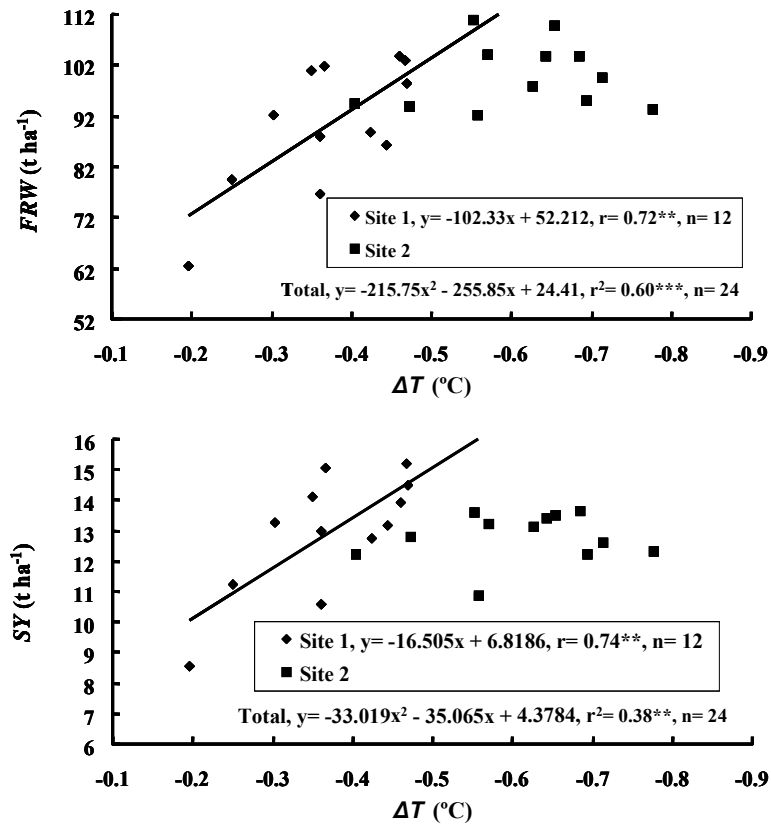
Figure 1. Relationships between *ΔT* and yields (*FRW*, *SY*) for each site and the combined data.
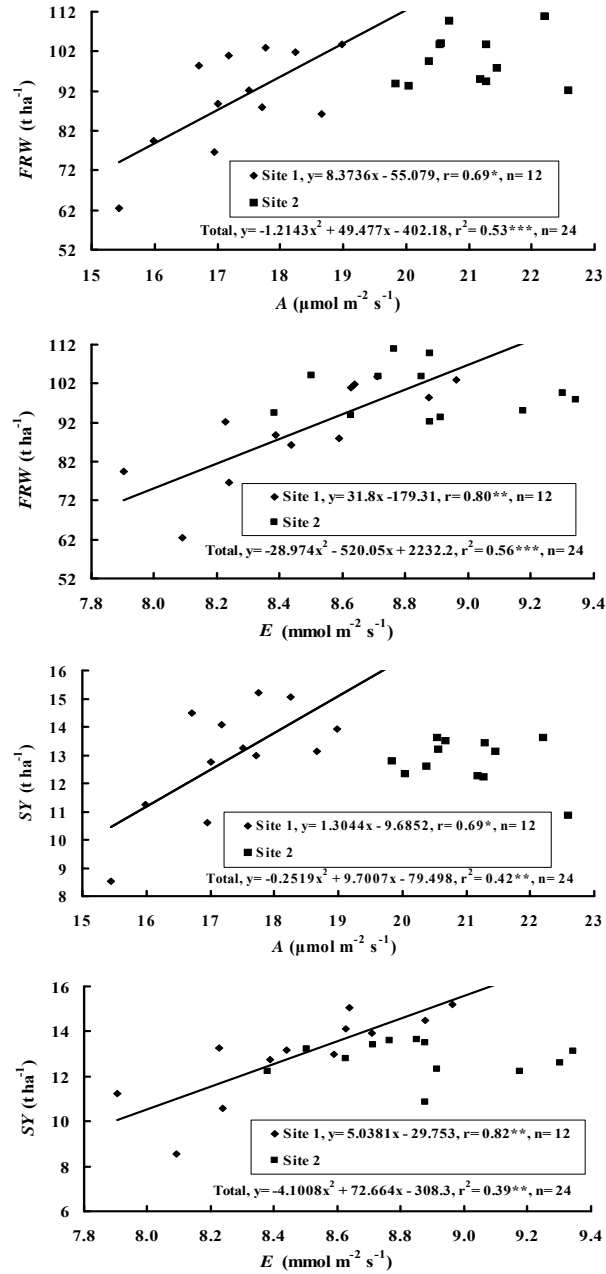**, ***: P<0.01, P<0.001, respectively.

Figure 2. *A* and *E* relationships with yields (*FRW*, *SY*) for each site and the combined data.
*, **: P<0.05, P<0.01, respectively.

SPAD readings were positively correlated with *FRW* and *SY* in Site 1 (r= 0.78 and r= 0.72, respectively, P<0.01, n=12). In Site 2, excluding an outlier, *FRW* was strongly and negatively correlated with *SPAD* (r= -0.87, P<0.001, n=11). A weaker but significant, negative correlation was found between *SPAD* and *SY* (r= -0.71, P<0.01, n=12). Quadratic functions were the best-fitted curves when the data of both sites were combined (Figure 3). The optimum *SPAD* reading for maximum yield was estimated at 44.7 and 44.0 for *FRW* and *SY*, respectively.

LAI was significantly correlated with yields only in Site 2, which had the highest average *LAI* (Figure 3). However, the positive correlations were weak for both *FRW* and *SY* (r=0.58 and r=0.65, respectively, P<0.05, n=12). A weak positive correlation (r=0.50, P<0.05, n=24) was also found between *LAI* and *FRW* when data of the two sites were combined (Figure 3).

Significant correlations between physiological traits and root quality were found only in Site 2 (Figure 4). Sodium and *α-amino N* in roots were positively correlated with *A* (r=0.64 and r=0.58, respectively, P<0.05, n=12). A positive correlation between *α-amino N* and *SPAD* was also evident (r=0.68, P<0.05, n=12).

Discussion

The two experimental sites had contrasting pedo-climatic conditions resulting to significant G×E interactions for both yield and quality traits (Tsialtas and Maslaris, 2009).

Physiological traits were strongly controlled by the environment while the genotypic effects on the instantaneous physiological measurements were small. However, the small physiological differences can result to significant yield and quality differences among cultivars since quantitative and qualitative traits are the cumulative effect of small, long-term physiological differences.

Leaf to air temperature difference (*ΔT*), a measure of leaf cooling ability *via* transpiration, showed strong correlation with yield in Site 1. Under the warm and dry conditions of that site, cultivars with cooler leaves had higher *E* and *A* and finally, higher yields. *ΔT* is a reliable and rapid indicator of crop water relations, useful for screening genotypes tolerant to water shortages (O'Toole et al., 1984; Kumar and Singh, 1998; Silva et al., 2007). However, a cooler leaf was not advantageous for higher productivity in Site 2, which is a favorable one for sugar beet growth. Optimum *ΔT* values for maximum *FRW* and *SY* were -0.59 ºC and -0.53 ºC, respectively. These values could be used as a threshold for selecting high yielding cultivars or as an indication of non-stressed growth conditions for sugar beet.
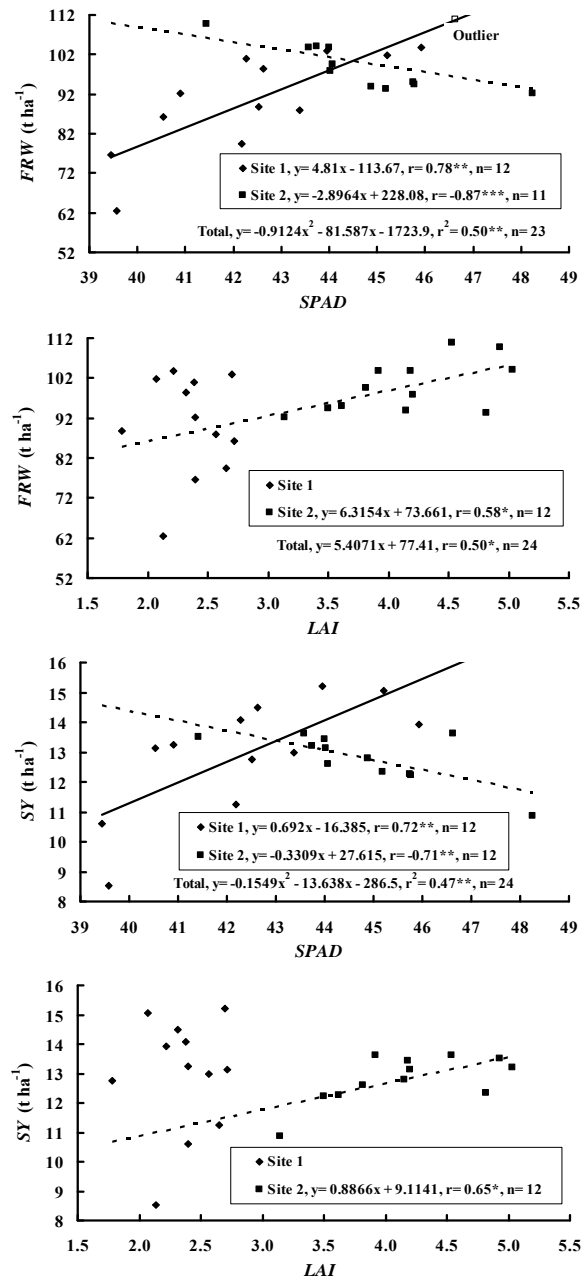
Figure 3. *SPAD* and *LAI* relationships with yields (*FRW, SY*) for each site.
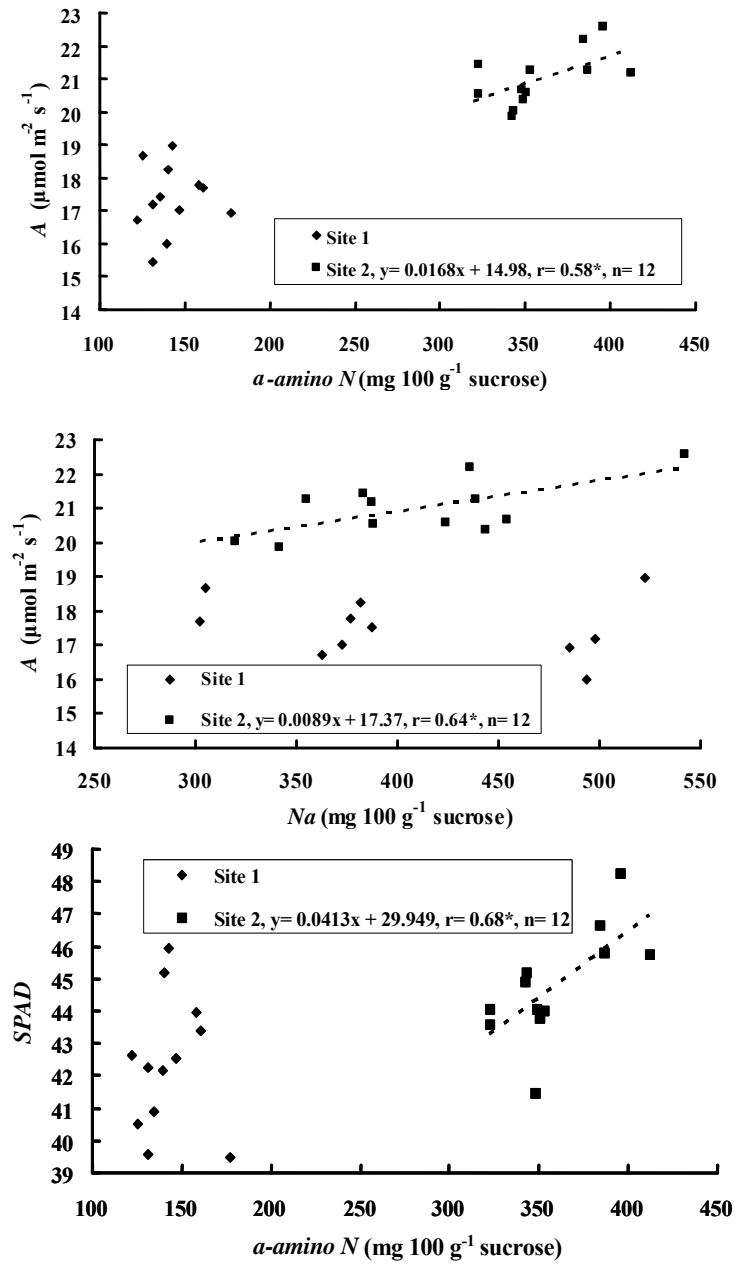*, **, ***: P<0.05, P<0.01, P<0.001, respectively.

Figure 4. Relationships of root *Na* and *α-amino N* concentration with *A* and *SPAD* for each site.
[*]: P<0.05.

It is reported that yield improvements could be derived from cultivar selection for higher photosynthesis (Jiang et al., 2003; Long et al., 2006). Although a higher A is considered to contribute to genotypic performance in favorable environments (McAllister et al., 1998; Arntz et al., 2000), this was not evident in our study. Higher yields were related with higher A only under the stressful conditions in Site 1, an effect controlled by ΔT. Optimum A for maximum yields was estimated at 19-20 μmol m^{-2} s^{-1}, a value close to the seasonal maximum A recorded in Mediterranean environments (Tsialtas and Maslaris, 2008a). In dry regions, sugar beet yield is strongly determined by the available water which is transpired through the leaves (Jaggard and Qi, 2006). This was confirmed by the positive correlation between E and yields in Site 1. Cultivars having a deeper and/or a denser rooting system can access more soil water and thus, they can support higher E, lower ΔT, and higher A and finally, they yield better (Lopes and Reynolds, 2010). However, works on sugar beet cultivar variation in root characteristics related to soil water accessibility are lacking. The optimum E value for maximum FRW and SY were estimated at 8.97 mmol m^{-2} s^{-1} and 8.86 mmol m^{-2} s^{-1}, respectively.

$SPAD$ readings have been proved a reliable, non-destructive and rapid assessment of leaf chlorophyll and N in sugar beets (Malnou et al., 2008) and a reading of 38 was set as the lower limit indicating N adequacy (Tugnoli and Bettini, 2000; Tsialtas and Maslaris, 2008b). Since $SPAD$ is positively related with A (Kumagai et al., 2009), a finding confirmed in Site 2, it was proposed as a rapid and heritable trait for screening genotypes with a good photosynthetic machinery and thus, for selecting high yielders under stress conditions (Giunta et al., 2002; Silva et al., 2007; Nigam and Aruna, 2008; Songsri et al., 2008). Sugar beet genotypes, which maintained the greenness of their foliage under drought stress, yielded better (Ober et al., 2004; Ober et al., 2005). A previous work by Pulkrábek et al. (2001) failed to identify the high yielding genotypes using $SPAD$ in sugar beet. In Site 1, positive correlations between $SPAD$ and yields (FRW, SY) showed that staying green under stressful conditions contributes to higher yields. On the contrary, the respective correlations in Site 2 were negative indicating that high investment in leaf chlorophyll is not beneficial in favorable environments since it occurs on expense of a higher growth rate (Poorter et al., 1990; Westbeek et al., 1999). However, in Site 2, higher yields were related with higher LAI values, with high yielders having $LAI > 3.5$-4.0, which was proposed as the optimum for maximum light interception (Jaggard and Qi, 2006). A negative correlation between $SPAD$ and LAI in Site 2 indicated that a high yield in that site was associated with a less green but a denser canopy.

In Site 2, parameters related to photosynthetic machinery (*A* and *SPAD*) were positively related with root *α-amino N* concentration, an organic form of *N*, which supports growth and associates with *N* concentration in sugar beet parts (Pocock et al., 1990). Sodium accumulation in root was positively related with *A*, a finding confirming the positive effects of *Na* on sugar beets grown on *Na*-poor soils (Milford et al., 1977) and providing an explanation for the negative relationship between selective absorption of *K* over *Na* and yields reported previously for Site 2 (Tsialtas and Maslaris, 2009).

Conclusions

In stressful Site 1, *ΔT*, *A*, *E* and *SPAD* were positively related with yields (*FRW* and *SY*). Cultivars, which transpired more, had cooler and more photosynthetically active leaves thus, they yielded better. *ΔT* and *SPAD* can be used as reliable and rapid screening of high yielders under stress conditions. In Site 2, where the conditions were favorable for sugar beet growth, yields were positively related with *LAI* but negatively with *SPAD*. Under these conditions, high investment in chlorophyll is not beneficial for high yields. However, *SPAD* maintained its discriminative ability to screen for high yielders.

Acknowledgments

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