

Association of agronomical, morphological and anatomical traits with compensatory effect of stem reserve mobilization in common wheat genotypes under drought stress

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Abstract: Enhanced dry matter remobilization from vegetative tissues under terminal drought contributes to wheat grain yield. Two-year field study was conducted with aim to determine the range of compensatory effect (CE) based on stem dry matter remobilization in defoliated (10 days after anthesis) and intact plants of 61 wheat (*Triticum aestivum* L) genotypes included three groups: 17 standard genotypes, 27 F_{4,5} families and 17 parent genotypes (only second season) used to make F_{4,5} families. Agronomical, morphological and anatomical traits which influence the CE were analysed. Over two seasons CE was affected by environmental conditions. On average across standards and F_{4,5} families CE was higher in the first season when mean stress intensity index of 0.145 (quantified as mild stress) was lower than 0.278 (quantified as moderate stress) obtained for the second season. Genotypes with higher number of spikelets and grains per spike, as well later flowering showed be yield loss compensation. Stem biomass and peduncle anatomical traits which determine potential for accumulation and remobilization of dry matter, such as stem wall thickness, photosynthetically not active parenchyma and number of large vascular bundles, showed positive correlation with CE. Although compensation of yield loss might be improved through breeding process (our F_{4,5} families had slightly higher mean CE than their parents under moderate stress), it does not mitigate the effect of post-anthesis drought in great extent (up to 38.4%).

Keywords: wheat, stem dry matter, defoliation, compensation, traits.

Riassunto: La mobilitazione della sostanza secca per traslocazione dai tessuti vegetali sotto condizioni di siccità nel periodo finale contribuisce alla resa della granella nel frumento. Due anni di studio sul campo sono stati condotti con lo scopo di determinare la gamma di effetti compensatori (CE) basati sulla mobilitazione della sostanza secca nel culmo in piante defogliate (10 giorni dopo l'antesi) e intatte di 61 genotipi di frumento (*Triticum aestivum* L) inclusi in 3 gruppi: 17 genotipi standard, 27 famiglie F4:5 e 17 genotipi parentali (solo in seconda stagione) utilizzati per costituire le famiglie F4:5. Sono stati analizzati i tratti agronomici, morfologici e anatomici che influenzano i CE. In due stagioni i CE sono stati influenzati da condizioni ambientali. In media tra gli standard e famiglie F4:5 i CE erano più alti nella prima stagione quando l'indice di intensità di stress medio di 0.145 (quantificato come stress leggero) era superiore a 0.278 (quantificato come stress moderato) ottenuto per la seconda stagione. I genotipi con maggior numero di spighe e granella per spiga, nonché la fioritura tardiva hanno mostrato una migliore compensazione per la perdita di resa. La biomassa del culmo e i tratti anatomici del peduncolo che determinano il potenziale di accumulazione e traslocazione della sostanza secca, come lo spessore della parete del culmo, il parenchima fotosinteticamente non attivo e il numero dei grandi fasci vascolari, hanno mostrato una correlazione positiva con i CE. Sebbene la compensazione della perdita di resa possa essere migliorata attraverso il processo di miglioramento genetico (le nostre famiglie F4:5 hanno un CE leggermente più elevato rispetto ai loro parentali sotto stress moderato), non ha mitigato l'effetto della siccità post-antesi (fino al 38.4%).

Parole chiave: frumento, sostanza secca del culmo, defogliazione, compensazione, caratteristiche.

INTRODUCTION

Wheat growth and development is affected by drought during both vegetative and generative phase and grain filling stage is critical for grain yield formation (Cattivelli *et al.*, 2008). It is widely

accepted that there are two sources for grain carbohydrates: filling through leaves and spikes (Maydup *et al.*, 2010) and the carbohydrates derived from photosynthesis prior to anthesis and during post-anthesis period, stored in the stem and remobilized to grains during filling stage (Bonnet and Incoll 1992; Ehdaie *et al.*, 2006). Stem reserve mobilization to ear is present in wheat plants under optimal growth, whilst drought and heat stress considerably enhance this process (Bell and Incoll, 1990; Wardlaw and Willenbrink,

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2000). Mobilization efficiency was observed to be higher in the internodes of tolerant wheat cultivar than in sensitive one, both under control and stress conditions (Gupta *et al.*, 2011). Plants have a variety of mechanisms for adaptations to environmental stress caused by abiotic and biotic factors. In the literature compensation is described as an adaptation of plants to environmental changes (Wenkert *et al.*, 1978). As a result, compensatory effect can be seen through adaptation mechanisms to nutrient uptake (Lambers and Porter, 2004), soil pH (Kochian *et al.*, 2004) or water absorption (Gullo *et al.*, 1998). Recently, Ma *et al.* (2014) reported differences between two wheat genotypes (one suitable to irrigation and one to rainfed conditions) in compensation effect, based on stem dry matter remobilization under drought conditions imposed after anthesis.

Numerous studies brought results on variation of wheat genotypes capacity to accumulate reserves in vegetative organs (Dreccer *et al.*, 2013; Ehdaie *et al.*, 2006; Ruuska *et al.*, 2006; van Herwaarden and Richards, 2002). As highlighted by Cruz-Aguado *et al.* (2000) dependence of yield on available stem reserves should be clearer under photosynthesis-limiting conditions in plants which have some quantity of stored compounds. In addition to morphology, stem reserve storage capacity has been recently associated with anatomical traits such as the total amount of pith-fill in the upper stem internode or stem wall characteristics (Saint-Pierre *et al.*, 2010; Dreccer *et al.*, 2013). Important role of stem reserves in the supply of carbohydrates to the wheat grains is well documented (Blum *et al.*, 1994; Ehdaie *et al.*, 2006), thus improved ability to store and remobilize them to grain is a desirable criterion in wheat breeding programmes targeted to regions with frequent terminal drought (Dreccer *et al.*, 2009).

The aim of presented study was to evaluate the genotypic variation in compensatory effect of stem dry matter remobilization to grains of 61 bread wheat genotypes under conditions of terminal drought which was simulated by plants defoliation after anthesis. Furthermore, the aim was to study the relationship between compensatory effect and different stem-related traits.

MATERIALS AND METHODS

Genotypes

The seeds of 61 winter and facultative wheat (*Triticum aestivum* L) cultivars and breeding lines were taken from the seed stock of Maize Research Institute Zemun Polje, Serbia (MRIZP).

Experimental plant material included three groups: 17 standard genotypes (STA), 27 F_{4.5} families (FAM) and 17 parent genotypes used to make F_{4.5} families (PAR). Genotypes of PAR group were studied only in the second year of investigation. Data on origin, parentage and criteria for crossing of tested genotypes was published elsewhere (Dodig *et al.*, 2016a).

Field experiments and measurements

The experiment was conducted at the experimental station of MRIZP (44°52'N and 20°19'E, 82 m ASL) during two growing seasons (2010/11 and 2011/12). In both seasons wheat genotypes were planted in late October on a slightly calcareous chernozem soil and harvested in late June following year. Seeding rate was 450 seeds m⁻², whilst ten rows of 1 m length were spaced at 20 cm. From March until the beginning of May (the end of stem elongation stage) plants were irrigated manually to maintain water content >50% of field capacity, with aim to prevent reduction of reserve accumulation and storage capacity in stems. Standard growing practices for growing wheat were applied. In defoliated plants (DP) all leaf blades were cut 10 days after anthesis (10 DAA) with aim to simulate drought stress (Blum *et al.* 1983), whilst control plants (CP) were intact. This approach could simulate also other abiotic or biotic stress such as disease attack on leaves which effects performing photosynthesis. Meteorological data are shown in Tab. 1.

Uniform plants flowering at the same day within genotype were tagged for sampling. First sampling of five plants was done 10 DAA, while five plants per CT and DP treatment were sampled at the stage of physiological maturity. At the first sampling stem height (SH) and peduncle length (PDL) were measured. Stem specific weight (SSW) was calculated as the ratio of stem dry weight to stem length. Peduncle share (PDS) was calculated as the ratio of its length to stem length. Dry mass of main stem (BMS) was measured 10 DAA and at harvest, after drying of

Month	Temperature (°C)		Precipitation (mm)	
	2011	2012	2011	2012
March	8.0	8.9	18.6	2.5
April	14.4	13.5	14.1	73.3
May	17.5	17.3	94.8	81.8
June	22.2	24.3	23.0	16.1
Mean/Sum	15.5	15.9	150.5	173.3

Tab. 1 - Meteorological data for two wheat growing seasons.
 Tab. 1 - Dati meteorologici di due stagioni di coltivazione del frumento.

plant material at 70°C for 48 h. Number of days to flowering (DTF) was estimated from the January 1st to 50% anther extrusion on the main spike. Following anatomical and biochemical peduncle parameters were analysed after sampling at 10 DAA: the number of bigger vascular bundles (BBN), total phloem area per stem section (PASS, mm²), stem wall thickness (SWT, µm), area of photosynthetically not active parenchyma (PA, mm²), lignified tissue share in total tissue (LTS, %), water soluble carbohydrate content (WSC, mg WSC 100 mg⁻¹ dry weight) and water soluble carbohydrate specific content (mg WSC cm⁻¹ length). Measuring of the traits was described in more details and their mean values across all genotypes were published elsewhere (Dodig *et al.*, 2016b, in press).

The number of spikelets (SN), number of grains per spike (GNS) and thousand grain weight (TGW) and harvest index (HI) were measured at maturity after final harvest.

Compensatory effect (CE, %) was estimated with following equation proposed by Ma *et al.* (2014):

$$CE = \frac{MDM(DP) - MDM(CP)}{Y(CP)} \times 100\%$$

where MDM(DP) is the amount of dry matter remobilized from stem in DP, MDM(CP) is the amount of dry matter remobilized from stem in CP and Y(CP) is the grain yield of CP. Positive CE value means that compensatory effect is associated with stress conditions and bigger CE value means a bigger compensatory effect that is provided by dry matter mobilization under a stressful condition compared with control, whilst negative CE value means that stress conditions did not have any effect on remobilization of dry matter from stem. Stress intensity index (SI) was estimated from: $(1 - (Xs2)/(Xns2))$, where Xs2 and Xns2 represent the mean grain weight across all genotypes evaluated under stressed (DP) and non-stressed conditions (CP), respectively.

Statistics

Summary statistics such as mean, standard deviation and coefficient of variation were used to describe the variability of the compensatory effect and drought indices in each season. Means between the genotype groups and seasons were separated by *t*-test, and letter groupings were generated by using a 5% level of significance. The correlation structure of the genotype by trait data table was visualized and interpreted by multivariate biplot techniques as described by Yan (2014). The interpretation of the biplot is based on

the “inner-product” principle (Kroonenberg, 1995). A positive correlation between two traits is represented by an acute angle between them and an obtuse angle represents a negative correlation. Separate biplots were constructed for CP and DP treatments. All computations and data visualizations were accomplished within the Minitab 17 software package.

RESULTS

Although the rainfall pattern in early spring (March–April) was rather different between the two years the additional irrigations during that period ensured sufficient water supply for biomass accumulation (Tab. 1). In general, growth conditions during anthesis and grain filling (May–June) were more favourable in 2011 than in 2012. Consequently, the SI values were 0.145 and 0.278 for 2011 and 2012, respectively. We quantified these values as mild and moderate stress conditions, as grain weight in defoliated plants due to stress treatment was almost double reduced in the second compared to the first season. Univariate statistical parameters were used to describe the variability of CE in tested genotypes. CE had a wide span within tested genotypes; in 2011 it ranged 1.7% - 32.2% and 0.7% -38.4% in 2012 (Tab. 2). Although PAR group was included in the study in 2012, the overall range between two years was similar. All groups showed high variability in CE; the coefficient of variation (CV) was >60% for all group/year combination. The highest CV was obtained for STA group in 2012 (107.2%). Most of tested genotypes performed big differences in CE between two seasons as suggested by Spearman’s rank correlation coefficient across STA and FAM ($r_s = -0.02$), but only STA group had significantly higher CE in 2011 than in 2012. In twelve F_{4.5} genotypes, CE in 2012 was higher than mean of parents used for crossing (Tab. 2).

The associations between CE and agronomical traits are illustrated by genotype by traits biplots. According to Yan (2014) a correlation coefficient between any two traits can be approximated according the cosine of the angle between their vectors when biplots explain ≥50% of the total variation. Presented biplots explained 50-75% of the total variation of the standardized data for all treatment/year combination. Similar biplot patterns showing associations of CE and agronomic traits were obtained for CT and DT in both seasons (Fig. 1). Among agronomic traits, CE was positively associated only with SN and GNS in DP in 2012, while the opposite relationship was observed for TGW and HI in both treatments and both seasons. Interrelationships between CE and morphological,

Compensatory effect (%)									
Standards			F4:5 families				Parents		
Name	2011	2012	Mean	Name	2011	2012	Mean	Name	2012
MRI 87/A	10.1	9.1	9.6	MRI S3/I	17.1	10.8 (18.3)	13.9	LI	5.5
MRI 87/B	7.6	4.0	5.8	MRI S4/I	7.4	22.9 (15.7)	15.2	L1/91	11.4
MRI 7	5.4	2.0	3.7	MRI S7/I	13.4	1.8 (10.4)	7.6	Donska s. dw.	15.3
MRI DK 1	13.9	8.1	11.0	MRI S10/I	26.5	11.9 (14.8)	19.2	Mexico 3	18.2
MRI DK 2	25.4	13.0	19.2	MRI S10/II	13.4	32.4 (14.8)	22.9	Avalon	25.9
MRI DK 3	4.6	7.4	6.0	MRI S11/I	14.3	5.6 (8.6)	10.0	Brigant	24.5
15HRWYT/07-224	23.0	4.3	13.7	MRI S12/I	1.7	18.7 (13.2)	10.2	Highbury	11.4
Pobeda*	27.2	5.1	16.2	MRI S134/I	25.0	9.5 (2.2)	17.3	NS 46/90	6.3
Renesansa*	3.8	2.0	2.9	MRI S134/II	21.7	2.0 (2.2)	11.8	WWMBC2	5.5
Zemunska rosa 1	16.4	2.8	9.6	MRI S268/I	2.8	3.2 (18.7)	3.0	NS 74/95	18.9
Apache	15.7	20.4	18.0	MRI D1/I	7.8	12.6 (6.6)	10.2	Benni m-fl.	7.4
Zemunska rosa 2	9.0	38.4	23.7	MRI D3/I	12.7	13.1 (14.8)	12.9	ZGKT 159/82	16.1
MRI AU 15	2.4	6.5	4.5	MRI D6/I	8.3	15.3 (1.3)	11.8	Lambri. Inia	16.0
ZP Olga	32.2	8.3	20.3	MRI D10/I	12.7	18.0 (9.9)	15.4	Florida	-1.1
MRI 146	16.2	24.9	20.6	MRI D10/II	5.2	2.9 (9.9)	4.1	Phoenix	8.1
MRI 162	26.3	1.4	13.8	MRI D11/II	12.0	18.6 (20.2)	15.3	Bezostaya 1	3.7
MRI 165	13.3	0.7	7.0	MRI D12/I	4.8	7.5 (9.0)	6.2	Mironov. 808	21.3
Mean	14.9a	9.3b	12.1	MRI D14/I	7.5	10.2 (5.0)	8.9	Pobeda*	5.1
SD	9.2	10.0	6.67	MRI D16/I	11.1	13.2 (4.2)	12.1	Renesansa*	2.0
CV (%)	62.0	107.2	55.0	MRI D18/II	2.5	5.6 (10.5)	4.1	Mean	11.7
				MRI D19/I	3.9	27.3 (5.7)	15.6	SD	7.8
				MRI D20/IP	5.3	6.1 (7.4)	5.7	CV (%)	67.2
				MRI D20/IH	20.7	6.1 (7.4)	13.4		
				MRI D21/I	19.7	2.5 (2.6)	11.1		
				MRI D22/I	7.2	2.0 (11.2)	4.6		
				MRI D25I	22.7	36.6 (5.1)	29.7		
				MRI D28/I	8.9	18.0 (13.3)	13.5		
				Mean	11.7a	12.4a (9.7)	12.1		
				SD	7.21	9.37	6.01		
				CV (%)	62.0	76.0	50.0		
Mean	13.3	10.9							

* Pobeda and Renesansa are standards, also parents for some crosses; they were included in both STA and PAR groups. SI = stress intensity index was calculated across all genotypes. Values in brackets represent mean CE obtained from parents used for crossing. Means of the genotype group over two seasons followed by different letters are significantly different at 0.05% levels of probability.

Pobeda e Renesansa sono standard, anche parentali per alcuni incroci; sono stati inclusi in entrambi i gruppi STA e PAR. SI = l'indice di intensità dello stress è stato calcolato su tutti i genotipi. I valori tra parentesi rappresentano la media CE ottenuta dai genitori utilizzati per l'incrocio. Le medie del gruppo del genotipo che sono seguiti da lettere diverse sono significativamente diverse con un livello di probabilità dello 0.05%.

Tab. 2 - Descriptive statistics for compensatory effect (CE) in standard genotypes (STA), F4:5 families (FAM) and parental genotypes (PAR) in 2011 and 2012.

Tab. 2 - Statistiche descrittive per l'effetto compensativo (CE) in genotipi standard (STA), famiglie F4: 5 (FAM) e genotipi parentali (PAR) nel 2011 e nel 2012.

anatomy and biochemistry traits are presented in Fig. 2. Since all traits were measured before defoliation was applied, there are no separate biplots for CP and DP as in a case of agronomy traits. In general, similar biplot patterns were obtained for both seasons. CE was highly positively associated with stem related traits such as BMS, SWT, BBN, PA and DTF in 2012 and with WSSC in 2011.

DISCUSSION

Based on the theories on mechanism of xerophytophysiology present in plants under various stress conditions (Xu, 2007), it has been proposed by Xu *et al.* (2009) that differential response of

internodes can be induced by drought conditions. In present study, the amount of remobilized dry matter in defoliated and control plants was calculated for the whole stem with aim to cover remobilization from all internodes. Imposed defoliation disrupted grain filling through leaf blades. Although some parts of the plants were still remained photosynthetically active after defoliation (e.g. spike and awns) we assumed that dry matter remobilization from stem was the main source of carbohydrates under such conditions. It is reported that 75 to 92% of pre-anthesis carbon stored in wheat stem was reallocated to mature grain under terminal drought stress (Yang *et al.* (2001). The defoliation was done

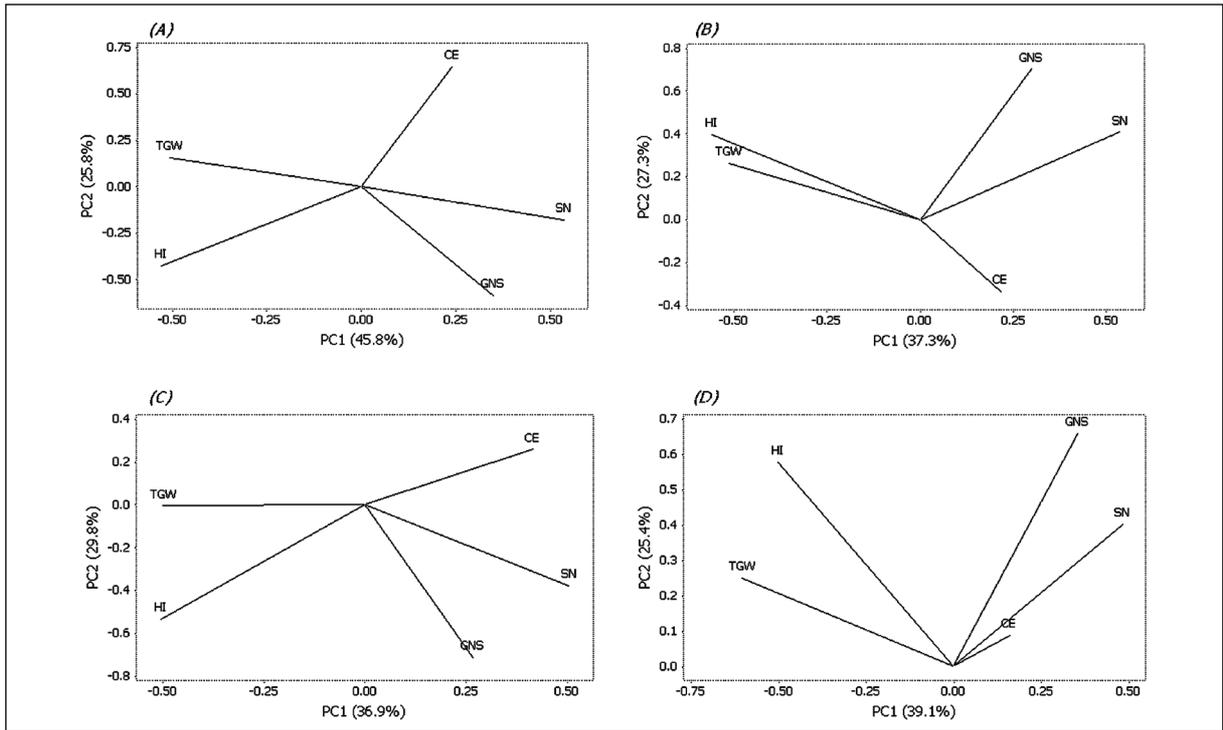


Fig. 1 - Genotype by trait biplot showing interrelationship between compensatory effect (CE) and agronomic traits based on mean values for 44 genotypes in CP (A), DP (B) in 2011 and CP (C) and DP (D) in 2012. Trait codes: SN = spikelets per spike, GNS = grains per spike, HI = harvest index, TGW = thousand grain weight, GWS = grain weight per spike.

Fig. 1 - Genotype by trait biplot mostra l'interrelazione tra effetto compensativo (CE) e tratti agronomici basati sui valori medi per 44 genotipi nel CP (A), DP (B) nel 2011 e CP (C) e DP (D) nel 2012. I codici delle linee: SN = numero di spighe per spiga, GNS = grani per spiga, HI = indice di raccolto, TGW = peso della granella in migliaia, GWS = peso del grano per spiga.

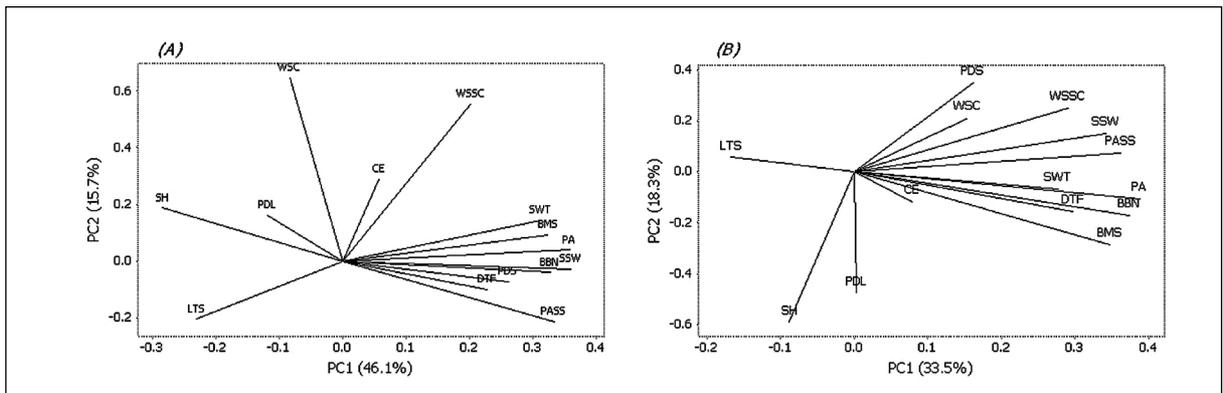


Fig. 2 - Genotype by trait biplot showing interrelationship between compensatory effect (CE), anatomical, morphological and biochemical traits based on mean values for 44 genotypes in 2011 (A) and 2012 (B). Measurements were done for CP and DP plants at 10 DAA. Trait codes: DTF (days to flowering), SH (stem height), PDL (peduncle length), PDS (peduncle share), SSW (stem specific weight), BMS (biomass per main stem), WSC (water soluble carbohydrates), WSSC (water soluble carbohydrate specific content), BBN (number of bigger vascular bundles), PASS (total phloem area per stem section), SWT (stem wall thickness), area of photosynthetically not active parenchyma (PA), lignified tissue share in total tissue (LTS).

Fig. 2 - Genotype by trait biplot mostra la relazione tra l'effetto compensativo (CE), caratteristiche anatomiche, morfologiche e biochimiche basata sui valori medi di 44 genotipi nel 2011 e 2012. Le misurazioni sono state realizzate per piante CP e DP a 10 DAA. Significato dei codici del grafico: DTF (giorni alla fioritura), SH (altezza del culmo), PDL (lunghezza del peduncolo), PDS (altezza del peduncolo), SSW (peso specifico del culmo), BMS (biomassa per culmo principale), WSC (carboidrati idrosolubili) WSSC (contenuto specifico dei carboidrati solubili in acqua), BBN (numero di fasci vascolari più grandi), PASS (area totale occupata dal floema per la parte del culmo), SWT (spessore della parete del culmo), area del parenchima non attiva fotosinteticamente (PA), porzione di tessuto lignificato (LTS).

10 DAA as it was shown that the stage of maximum mass and specific mass of the internodes ranged between 8 and 15 DAA (Cruz-Aguado *et al.*, 2000). High variation in CE among genotypes between two seasons confirmed large sensitivity of the accumulation and remobilisation of reserves to environmental conditions and source-sink status in wheat (Evans and Wardlaw, 1996). Based on higher stress intensity index in 2012, there was additional effect of weather conditions which enhanced the stress simulated by defoliation. On average over STA and FAM groups, under moderate stress condition dry matter remobilization from stem to grains compensated less yield loss than under mild stress condition (10.9 vs. 13.3%). However, FAM group showed slightly higher CE under moderate than under mild stress. In study by Ma *et al.* (2014) there was a large difference in compensation of grain yield loss by dry matter remobilization between two contrasting wheat genotypes under conditions of moderate drought stress, while their response by compensation was enhanced by severe stress (55-65% and 35-45% of field capacity, respectively). Growing conditions and drought stress treatments, also genotypes used in our study might be the reason for the obtaining the opposite results from mentioned study. In some genotypes in our study (12 out of 27) CE was higher than CE based on mean of parents used for crossing, suggesting that this trait could be manipulated through breeding. In presented study, although SN was more closely associated with CE in DP under moderate stress, positive association was recorded overall experiment, indicating that plants with bigger grain sink compensate more yield loss than those with smaller one, irrespective of water supply. Borrás *et al.* (2004) showed that growth of wheat grains is more sink- than source-limited, even in Mediterranean conditions (Cartelle *et al.*, 2006). Also, Madani *et al.*, (2010) suggested that the demand by the grain yield sink is a primary factor in determining stem reserve mobilization, which indirectly corresponds to our findings. Number of grains is largely determined during the stem elongation phase in relation to crop growth and partitioning (Fischer, 2011). Slafer and Savin (2006) concluded that yield depends far more on the number of grains than on the average weight of the grains. High correlation obtained between CE and BMS indicates that stem biomass is better predictor for compensatory effect than stem height (SH) and peduncle length (PL) which had neutral and negative association with CE over two seasons.

According to Moragues *et al.*, (2006) and Ehdaie *et al.*, (2006), stress tolerant landraces and genotypes partition more dry matter into their stems than non-tolerant wheat landraces. On the other side, stem specific weight (SSW) which determines storage capacity of plant (Blum *et al.*, 1994) as well as PDS showed weak association with CE in both seasons in our study. Strong positive association of CE with days to flowering (DTF) identified under moderate stress indicates that late flowering genotypes accumulated bigger amounts of dry matter in stem in comparison to early ones. Extended stem elongation phase might be targeted as desirable trait (Slafer *et al.*, 2001), which is current interest in wheat and barley breeding (Dreccer *et al.*, 2013). Negative association of CE with TKW suggests that for filling large kernels stem reserves was not sufficient and plants used other source such as spike or awns (Madani *et al.*, 2010), which still remained photosynthetically active (green) after leaves removing.

Ma *et al.*, (2014) suggested that upper internodes are physically closer to grain sink what might be the reason for their enhanced activity in dry matter remobilization. According to Wardlaw and Willenbrink (1994) and Gebbing (2003) morphology of the peduncle is related to grain yield. Based on high correlation between CE and stem wall thickness (SWT) (Fig. 2) seems that stem capacity determines remobilization of stored assimilates which compensate the yield loss under drought stress. Moreover, results of presented anatomical study showed that CE was positively correlated with number of large vascular bundles (BBN), total phloem area (PASS) and area of photosynthetically not active parenchyma (PA) which represents large parenchyma cells, indicating that higher potential for remobilization of stored dry matter to grains under moderate stress resulted in greater compensatory effect in 2012. These results and strong positive correlation of WSSC with CE confirms findings by Saint-Pierre *et al.*, (2010) who determined that pith filling in the upper stem internode and total amount of pith-fill was highly correlated with the total content of water soluble carbohydrates per stem under both water deficit and irrigation. On the other hand, based on strong negative association of lignified tissue share in total tissue (LTS) with CE in our study, seems that presence of lignified tissue in the stem is undesirable trait that limits storage and remobilisation of stem dry matter. Weak (positive) association was recorded between the rest of traits such as SSW and PASS and CE in both seasons. In conclusion, differential response of genotypes

to defoliation over two seasons indicates that stem dry matter remobilization is strongly affected by environmental conditions. Large genetic variations in compensation among tested genotypes indicate that compensatory effect to yield loss under postanthesis drought stress might be enhanced through breeding process. Some of our F_{4,5} families had higher CE than mean of parents used for crossing. However, this could be further improved as it does not mitigate the effect of post anthesis drought in greater extent (less than 40%). Bigger grain sink in terms of number of spikelets has been shown to enhance compensation from stem reserve mobilization irrespective of exposure to defoliation. Presented study clearly showed that stem biomass plants, stem wall thickness, area of photosynthetically not active parenchyma and number of bigger bundles contributes to yield loss compensation.

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