Breeding for high stem water-soluble carbohydrate reserves

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Introduction

Wheat stems range from solid (entirely pith filled) to hollow (no internal pith). The pith in the solid stems consists of undifferentiated parenchymatous cells which accounted for the 11 percent of total stem dry weight at 10-14 days after anthesis in a study conducted in F4 plants derived from winter wheat crosses grown in a greenhouse. Those cells contributed to 13 percent of a total of 0.67 g of sugar in the entire stem. Sugars accumulated in the stems as reserve are water-soluble carbohydrates (WSC) which could be potentially remobilized and transported to the developing grain.

Previous studies have been contradictory about the relationship between solid stems and grain yield. Ford et al. (1979) conducted a study in greenhouse and irrigated field conditions to correlate stem anatomy, concentration of ethanol soluble carbohydrates, and yield on solid and hollow stemmed selections which came from ten crosses between winter wheat lines contrasting in the solid stem trait. The concentration of carbohydrates was slightly though not significantly greater in the solid than in the hollow stems. Even without differences in carbohydrate concentration, the amount of soluble carbohydrates per unit length of stem was significantly greater in the solid stems than in hollow stems because solid stems had greater weight per unit length. However, total carbohydrates per stem did not differ between the two selections because solid stems were shorter and narrower than hollowed ones. Finally, the authors found no differences in grain yield for solid and hollow stemmed groups.

A good capacity for stem reserve and remobilization has been proposed as a drought adaptive trait in a conceptual model for drought tolerance (Reynolds et al., 1999) since contribution to grain yield from assimilation before anthesis is greater under terminal drought. Theoretically, genotypes which accumulate a large amount of WSC in the stem may be able to relocate more carbohydrates to the grain than genotypes with less stem carbohydrates concentrations when the supply of carbohydrates by photosynthesis is limited. Therefore, selection for greater stem storage of WSC could result in improved grain-filling and increased yields when terminal drought decreases carbon assimilation.

Objectives

Genotypes with differences in expression of stem solidness were evaluated to assess variation in stem storage capacity and its relationship with yield under two contrasting environments (drought and irrigated). We tested the hypothesis that solid stems contribute to a higher accumulation of reserves resulting in higher yields. The ultimate goal was to identify morphological traits that contribute to improve grain yield with potential use in wheat breeding.

Materials and Methods

Field experiments

Genotypes used in this study came from CIMMYT's spring bread wheat breeding program for dry areas. A total of five parents were combined to create a gradient in the expression of stem solidness and thickness, as well as in the expression of physiological and agronomic traits.

Plots were sown in Mexico (Cimmyt Obregon Experimental Station, Yaqui Valley, 27° 20'N, 109° 54'W, 38 m asl) following an α-lattice design with two replicates. Genotypes were planted in late November and harvest in April. Pesticides and fungicides were applied as necessary.

Two irrigation regimes were applied. For the irrigated treatment, plots were irrigated when approximately 50% of available soil moisture was depleted according to gravimetric determinations. The reduced irrigation treatment (drought) was imposed to induce water deficit stress.

Yield was measured by machine-harvesting an area of 4.8 m^2.

Stem solidness estimations

Six spike-bearing culms were randomly selected from each plot at anthesis plus 10 days stage. The length of total stem, peduncle, upper stem internode (the internode below the peduncle), and lower internodes was determined. Diameter of the upper stem internode was determined with a digital external screw-type micrometer.

For stem solidness estimations, stems internodes were cut across the middle point of the upper stem internode and the thickness of the wall (wall + pith fill) was determined with the digital micrometer. The amount of pith filling the stem at the upper stem internode was calculated considering stem diameter, wall thickness, and the length of the internode.

WSC estimations

Twelve randomly selected main stems for each plot were cut at the ground level 10 days after anthesis. It was previously demonstrate that the maximum in stem weight and carbohydrate concentration occurs 10-14 days after anthesis and it is followed by a rapid decline in carbohydrate concentration during grain filling. Samples were oven dried at 75°C for 48 h to constant weight. Above-ground dry-matter was separated by hand into stems (stem + leaf sheath + leaves) and heads, weighed and ground (UDY 3010-030) to pass a 0.5 mm screen.

Near-infrared reflectance spectroscopy (NIRS) was used to estimate WSC concentration (NIRSystems 6500; Foss NIRSystems Inc.). Predictive equations were developed and cross-validated using the results of chemical analyses (Anthrone method). WSC concentration was calculated on a dry weight basis (mg g^{-1} dry weight) and also on an area basis (g m^{-2}).

Statistical analysis

Data were analyzed by mixed effects analysis of variance using PROC MIXED in SAS (SAS Institute, Inc., 2004).

Results

Significant genetic variation in stem solidness was found in the genotypes selected for this study. There was a gradient in the amount of pith fill in the stems from solid (entirely pith filled) to hollow stems (no internal pith). Expression of stem solidness was affected by the environment; stem wall thickness was greater when plants were under irrigated environments than under drought (Fig 1).

There was no association between grain yield and stem wall thickness under irrigated or drought conditions. No association was found between anthesis date, and height and both upper stem wall thickness and WSC content on a dry weight basis.

The amount of pith fill in the upper stem internodes was highly correlated with WSC concentration under both drought and well watered conditions (Fig 2). Since WSC contributed to increase yields especially under drought (Fig 3), a positive correlation was found between grain yield and the amount of pith fill in the upper stem internodes ($p<0.001$; Table 1). The amount of pith-fill in this internode was calculated considering stem diameter, wall thickness, and the length of the internode. Under irrigated conditions, however, the relationship between pith fill in the upper stem internodes and grain yield was not significant ($p=0.47$).

Conclusions

We tested the hypothesis that solid stems contribute to a higher accumulation of reserves resulting in higher yields. The results fail to find a positive relationship between stem wall thickness and grain yield. Ford et al. (1979) reported similar yields for solid and hollow stemmed groups. In their study, the concentration of carbohydrates was slightly though not significantly greater in the solid than in the hollow stems and the amount of soluble carbohydrates per unit length of stem was significantly greater in the solid stems than in hollow stems because solid stems had greater weight per unit length. However, total carbohydrates per stem did not differ between the two selections because solid stemmed selections were shorter at maturity than hollowed ones. Ehdaie et al. (2006) suggested that the potential for stem reserve accumulation depends on both stem length and stem specific weight (stem weight/stem length). Thus, the capacity for WSC reserve would increase with longer stems and greater specific weight. Our study suggested that pith-fill would also contribute in determining the potential reserve accumulation. The amount of pith-fill at the upper stem internodes was highly correlated with WSC concentration, so it could be inferred that under same biomass production per area, solid stems would have more WSC available for translocation to the grains, resulting in higher yields.

Breeding for high WSC is possible considering the large broad sense heritability (H= 0.9) (Ruuska et al., 2006). However, high variation in the expression of stem solidness was observed across genotypes and environments. In this study, stem wall thickness was greater when plants were under irrigated environments than under drought. Previous studies had reported that stems were more solid when plants were exposed to high temperature or drought during stem elongation. Similar results were obtained in a field study testing spring wheats where stems were less solid in the irrigated environment than in the rain-fed environment. The subjectivity of stem solidness scoring and the variation in the expression of the character due to environmental conditions were identified as factors that complicate breeding for high- yielding lines with solid stems (Lanning et al., 2006). To overcome those limitations, marker-assisted selection for stem solidness had been propose as a tool to identify high-yielding breeding lines with solid stem genes (Lanning et al., 2006).

Our results suggest that breeding for solid stems could increase WSC by 70 mg per cm^3 of stem pith fill. The potential for obtaining high yielding solid stemmed cultivars is promising since no negative associations were observed between stem solidness and other agronomic traits. The expected benefits would be greater under water limited situations, where high stem WSC storage is critical for grain-filling. Stem diameter, wall thickness, and length of the internodes needed to be combined in an ideal plant ideotype for maximizing WSC reserves and as a strategy to break yield barriers under drought conditions.

References

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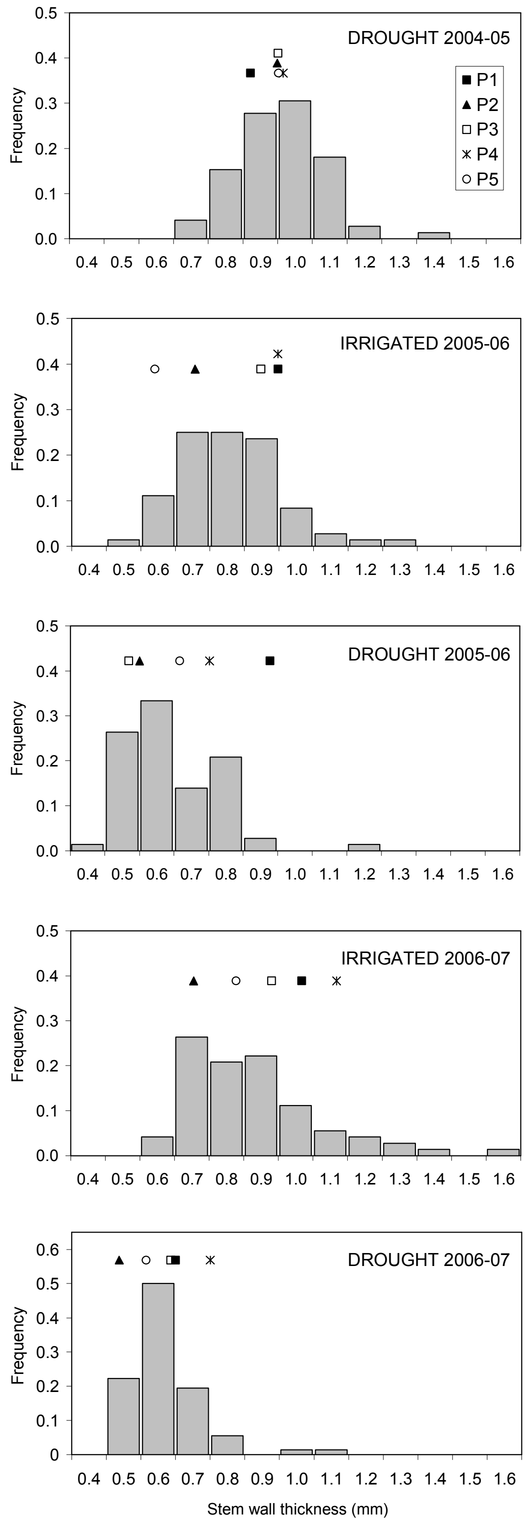

Figure 1: Distribution of stem wall thickness character, as an estimation of stem solidness in plants derived from crosses between BAVIACORA M 92 (P1), MILAN (P2), SST 57 (P3), PF74354//LD/ALD/4/2*BR12*2/3/JUP// PAR214*6/FB6631 (P4) and SHA3/SERI//SHA4/LIRA (P5). Plants were grown under irrigation and drought during two years.

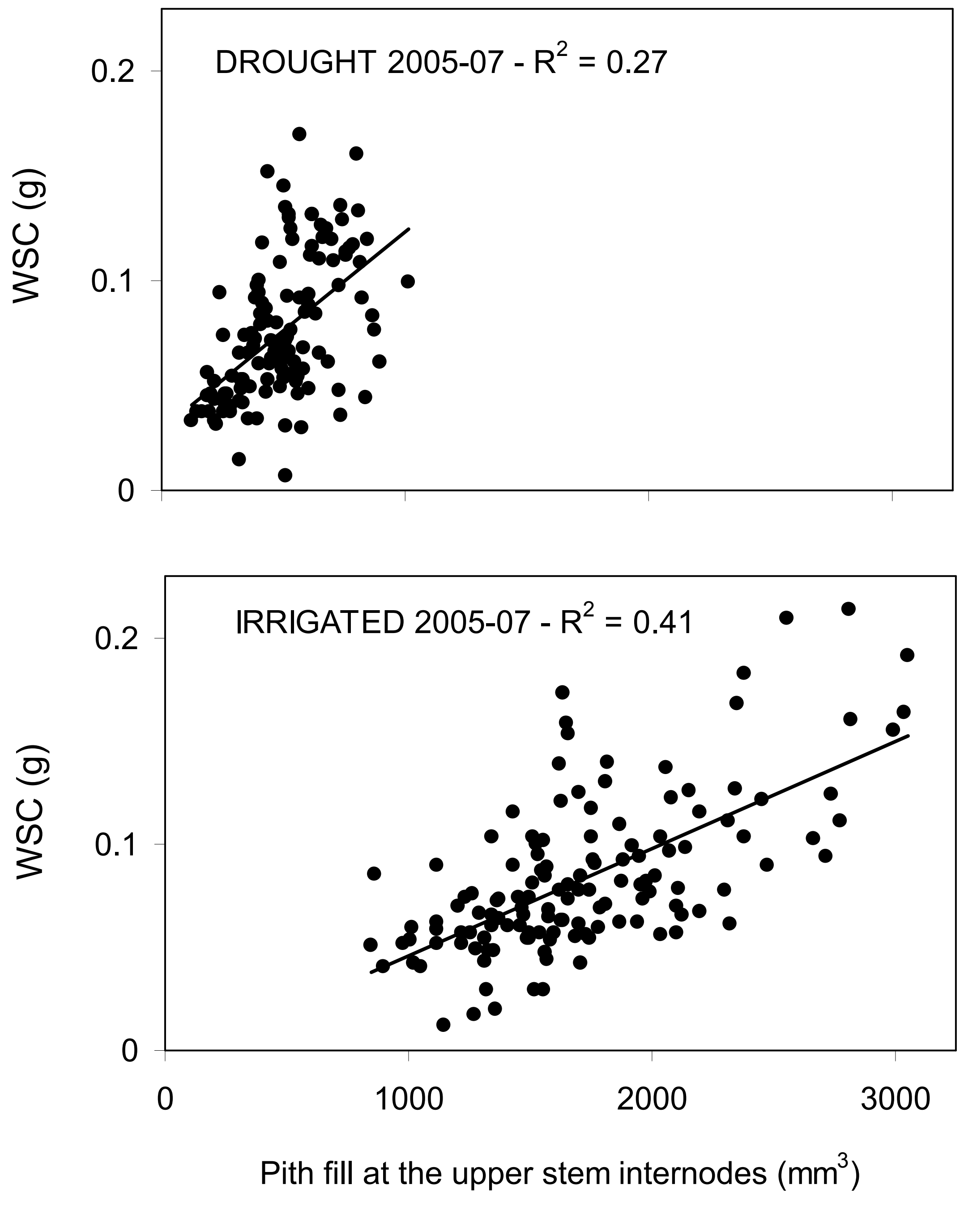

Figure 2: Relationship between the amount of pith fill at the upper stem internode and water-soluble carbohydrate (WSC) content in plants derived from crosses between genotypes contrasting in stem solidness growing under drought and irrigated conditions.

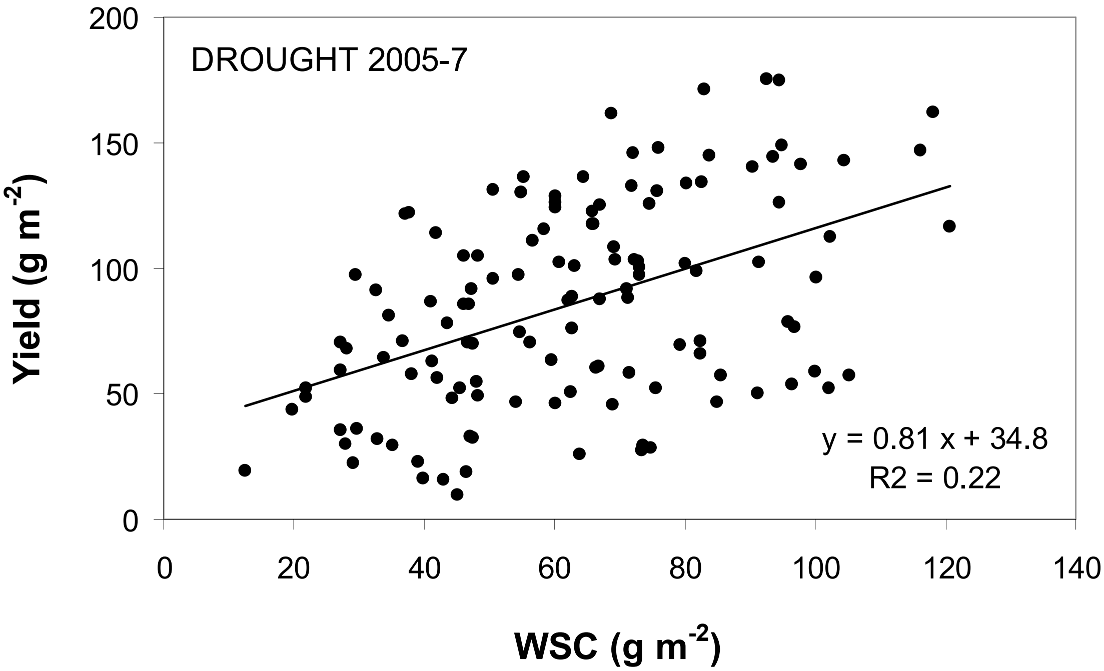

Figure 3: Relationship between water-soluble carbohydrate (WSC) and grain yield in plants derived from crosses between genotypes contrasting in stem solidness growing under drought.

Table 1. Mean, standard deviation, and correlation with grain yield for grain yield, stem length, upper stem internode properties, and stem water-soluble carbohydrates (WSC) for plants growing under irrigated and drought conditions during two years in Ciudad Obregon, Mexico.

		Grain yield	Stem length	Upper stem internodes					WSC at anthesis+10 days
				Length	Diameter	Wall thickness	Pith fill	WSC	
		--- g m^{-2} --	--- cm ---	--- cm ---	--- mm ---	--- mm ---	--- mm^3 ---	--- gr ---	--- g m^{-2} ---
Drought - 2005-07	Mean	85.23	50.51	11.72	3.01	0.56	517.67	0.08	61.37
	SD	41.35	9.65	3.27	0.54	0.12	217	0.03	24.45
	r-yld		0.75 **	0.34 **	0.41 **	-0.17 ns	0.33 **	0.19 *	0.35 **
Irrigated 2005-07	Mean	905	81.99	19.81	4.37	0.78	1760	0.09	99.57
	SD	135	10.08	2.52	0.57	0.19	550	0.04	34.02
	r-yld		-0.43 **	-0.37 **	0.20 *	-0.05 ns	-0.06 ns	-0.17 ns	-0.10 ns