Proceedings of the International
TRIGO (Wheat) Yield Potential
WORKSHOP 2015

**CENEB, CIMMYT, Cd. Obregón, Sonora, México
24-26th March, 2015**

Matthew Reynolds, Gemma Molero, Julie Mollins and Hans Braun (Editors)

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Abstract: The abstracts herein are of presentations by crop experts for the "TRIGO (Wheat) Yield Potential Workshop". Sponsored by SAGARPA's international strategic component for increasing wheat performance, under the Sustainable Modernization of Traditional Agriculture Program (MasAgro); and CRP WHEAT.

The event covers innovative methods to significantly raise wheat yield potential, including making photosynthesis more efficient, improving adaptation of flowering to diverse environments, addressing the physical processes involved in lodging, and physiological and molecular breeding. The workshop represents the current research of the MasAgro TRIGO project and CRP WHEAT that involves scientists working on all continents to strategically integrate research components in a common breeding platform, thereby speeding the delivery to farmers of new wheat genotypes.

Table of Contents

BREEDING METHODS

PARTITIONING

PHOTOSYNTHESIS

Program: TRIGO Yield Potential Workshop 2015

March 24th:	Update of Results on Wheat Yield Potential Research: Projects funded by SAGARPA-MasAgro and CRP-WHEAT		
OPENING	8:15	Enrique Martinez y Martinez, Minister of Agriculture, Mexico John Snape, CIMMYT Board Chair Hans Braun, Global Wheat Program Director	
BREEDING METHODS			
	9:00	Maria Tattaris	CIMMYT	Applications of an Aerial Remote Sensing Platform
	9:20	Sivakumar Sukumaran	CIMMYT	Genome-Wide Association Mapping for Adaptation to Agronomic Plant Density: A Component of High Yield Potential in Wheat
	9:40	Pedro Figueroa	INIFAP	Evaluation of the WYCYT in Five Irrigated Wheat-Growing Locations in Mexico
	10:00	Matthew Reynolds	CIMMYT	Pre-Breeding for Yield Potential: Summary of International Data from 2nd WYCYT and Performance of Pipeline Material
	10:20	DISCUSSION		
	10:40	**COFFEE**		
PARTITIONING			
	11:10	Daniel Calderini	Universidad Austral de Chile	Key Traits Associated with Potential Grain Weight in Selected CIMCOG Genotypes
	11:30	William Davies	Lancaster University	Hormone Concentrations Versus Yield Components: Why is this Information Useful
	11:50	John Foulkes	University of Nottingham	Achieving a Step-Change in Harvest Index in High Biomass Wheat Cultivars
	12:10	John Foulkes	University of Nottingham	Structural Requirements of Irrigated Spring Wheat to Avoid Lodging
	12:30	Gustavo Slafer	Uiversidad de Lleida	Towards the Manipulation of Floral Development to Increase Grain Yield in Wheat — A Physiological and Genetic Approach
	12:50	Gemma Molero	CIMMYT	Dissection of Yield Potential Related Traits: What Shall We Focus On?
	1:10	DISCUSSION		
	1:30	**LUNCH**		
PHOTOSYNTHESIS			
	2:30	Cándido López	COLPOS	Genetic Diversity of Light Interception Profiles in Modern Wheat Canopies
	2:50	Xinguang Zhu	PICB Chinese Academy of Science	Design Guided Engineering Higher Canopy Photosynthetic Light Use Efficiency
	3:10	John Evans	Australian National University	New temperature response parameters for wheat Rubisco
	3:30	Raju Datla	NRC	Targeting TOR Signaling to Improve Performance in Crop Plants
	3:50	**COFFEE**		
	4:10	Jose Luis Araus	Universitat de Barcelona	Photosynthetic Contribution of Ear to Grain Filling in Wheat: Comparison of Different Methodologies for Evaluation
	4:30	Martin Parry	Rothamsted	Discovery and Creation of Genetic Variation to Enhance Photosynthesis and Yield
	5:00	DISCUSSION		
	5:30	**ADJOURN**		
	7:00 - 9:00 Dinner in La Catrina			
March 25th:	Global Wheat Program Field Day (N.B this day involves participation from all Global Wheat Program and annual visitors) and Carne asada (5:00 - 9:00 p.m.)		
March 26th:	Brainstorming on how to achieve step changes in yield potential in the future (closed retreat among wheat yield potential experts).		

List of participants TRIGO Yield Potential Workshop 2015

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Applications of an Aerial Remote Sensing Platform

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Background
Advances in high-throughput field phenotyping technologies increase both breeding efficiency and the power of genetic dissection of yield and related traits. Remote sensing of spectral indices enables physiological and agronomic characterization at a large scale (e.g. Reynolds et al. 1998; Babar et al. 2006; Prasad et al. 2007) and can be applied in gene discovery (e.g. Reynolds et al. 2009; Pinto et al. 2010).

Airborne imagery has enough resolution to capture information at experimental plot level, while at the same time covering hundreds of plots in one take. Thus, aerial measurements can overcome limitations associated with poor spatial resolution of satellite imagery and temporal/environmental issues linked to ground-based measurements over large areas.

Measurements were made with a light-weight UAV over CIMMYT's experimental station in Ciudad Obregon, northern Mexico. Several indices were estimated and compared to equivalent ground-based measurements and, where possible, with yield and biomass. A thermal infra-red camera mounted on the UAV is used to estimate a thermal index, with relates to CT, while the multispectral camera calculates NDVI at the plot level. An investigation of the derivation of additional, more novel traits was also carried out using the multispectral and RGB cameras.

Summary of Applications and Results
Figure 1 presents examples of the thermal index and NDVI derived from the UAV against equivalent CT and NDVI measured at ground level. Airborne and ground-based measurements were made on the same day, or days as close as possible to each other. In general, correlations are strong between the two types of measurements, acting as a validation for the airborne derived indices. Correlations between the aerial thermal index and CT tend to be slightly lower than those of the NDVI index. This could be attributed to the higher variability of CT, due to environmental factors, particularly wind speed.
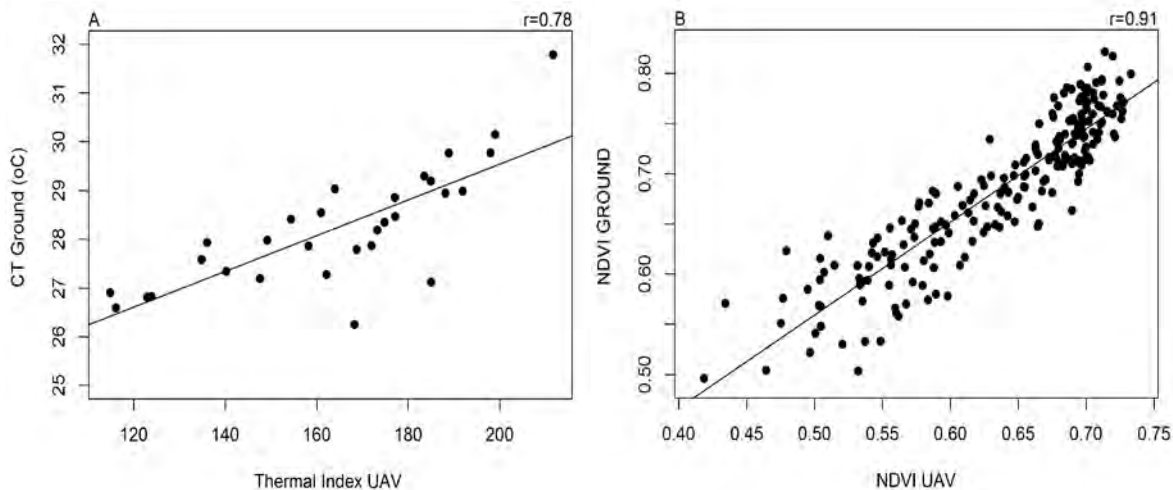
Figure 1a) Thermal index derived from the thermal imagery collected on-board the UAV against measurements of CT for irrigated trial under heat stress. b) NDVI derived from UAV measurements against NDVI ground-based measurements for trial under drought stress. Indices are derived from data from one reading.

The airborne derived thermal index and NDVI have been compared to yield and final biomass to determine how closely the airborne indices and these agronomic traits are related. Figure 2 presents a time series of the relationship between airborne derived UAV and biomass (2a) and yield (2b) over part of the growth cycle of a yield potential trial. As a comparison, the equivalent relationship between ground-based NDVI and yield/biomass is also shown.
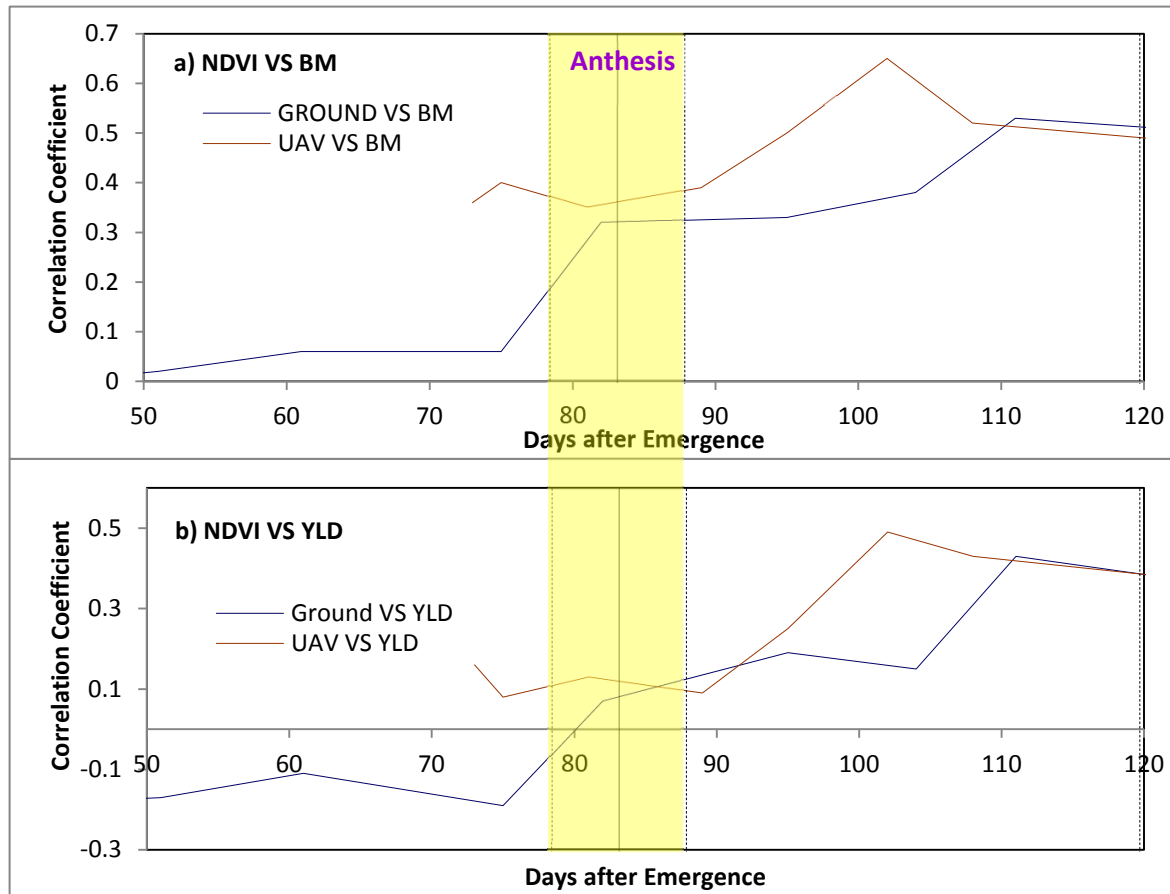
Figure 2: Time series of the correlation between NDVI and dry biomass weight (a) and yield (b) at harvest for UAV measurements (red) and ground-based measurements (blue) for a trial under yield potential conditions.

In general, the airborne measurements show a stronger relationship with yield/biomass compared to the ground-based measurements. This could be attributed to i) the ability of the airborne images, unlike the ground-based point measurements, to remove noise, such as non-vegetation pixels, as well as ii) the instantaneous measurement of plots via the airborne platform, which removes the confounding effect of temporal drift associated with ground-based readings in larger trials. This difference was seen to be significant in all cases excluding those from drought stress environments. Results support the application of airborne remote sensing techniques for high-throughput phenotyping. Time series like the ones above are useful at determining at which point in the growth cycle is it most efficient to make measurements, i.e. at which point in time index X best predicts yield or biomass.

The airborne platform also has the potential to estimate other, more novel traits, such as lodging, chlorophyll florescence (Zarco-Tejada et al. 2009; Chapman et al. 2014) and other traits. For example, Figure 3 shows various cross section images taken from a 3D point cloud created using a surface reconstruction algorithm applied to low level, overlapping, RGB images collected off nadir. From the 3D point cloud, it is possible to estimate height, LAI, and if the spatial resolution is high enough, other plant characteristics, such as such as spikes/m^2.
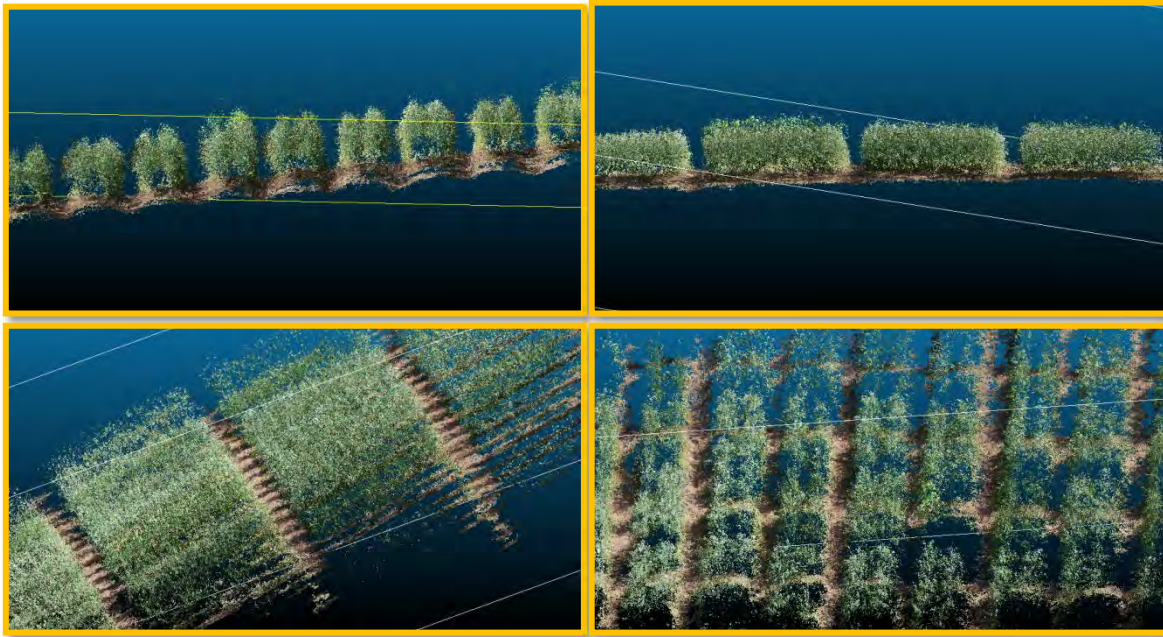
Figure 3: A 3D point cloud of wheat plots in the field created using a surface reconstruction algorithm applied to overlapping aerial RGB images taken at an angle of 85° and altitude of 10 m.

In addition, it might be possible to use low-level aerial imagery to estimate phenology of a plot, via changes in reflectance and plant architecture throughout the growth cycle. This method has already been applied using ground-based and proximal remote sensing methods (e.g. Deery et al. 2014). Figure 4 shows an estimation of spike count, taken from a snapshot of a low level multispectral image. The estimation was calculated via a multistage classification process based on the pixel values.
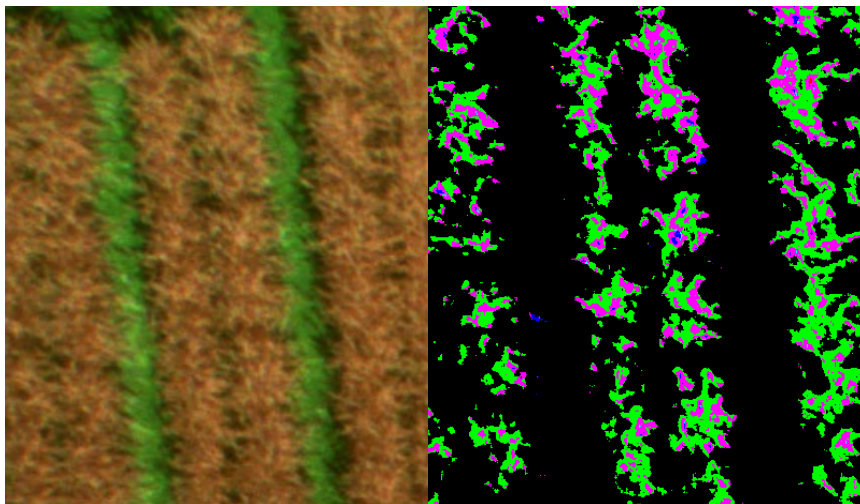
Figure 4 Left: Section of a multispectral image taken at 10m altitude of wheat plots in the field. Right: Classification of image on left with aim of detecting spikes in the plot, based on the pixel values of the image. The purple area denotes the detected spikes.

In summary, the aerial remote sensing platform can be applied as a high-throughput phenotyping tool for trait estimation and selection, with such large-scale measurements increasing the probability of genetic diversification in selections. It also has the potential to be utilized for smaller scale measurements to estimate traits that require higher resolution. To optimize these methods, high-throughput automated analysis procedures must be developed in order to process the high volumes of data that are generated and applied.

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Genome-Wide Association Mapping for Adaptation to Agronomic Plant Density: A Component of High Yield Potential in Wheat

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Background

Increasing yield potential *per se* still remains a major objective of crop improvement programs worldwide (Braun et al. 2010; Reynolds et al. 2012). A significant proportion of yield potential of CIMMYT's semi-dwarf spring wheat lines can be explained by genetic variability for adaptation to agronomic planting density (Reynolds et al., 1994a). Earlier released lower yielding lines showed a higher yield response to reduction in interplant competition—i.e. treatments that increased light penetration to the lower canopy from boot stage onwards, as well as treatments that combined increased light penetration with decreased below ground competition—than more modern higher yielding varieties. The results indicated the sensitivity of low yielding genotypes to plant density and the potential of some high yielding genotypes to perform well both under high interplant competition and reduced interplant competition. In other words high yield potential (HYP) genotypes respond less when interplant competition was reduced than the earlier released low yield potential (LYP) lines. Little is known about the genetic basis of the adaptation of wheat plants to agronomic density, which is significant considering that it is not something that would have been selected for in nature, interplant competition of single plants being of clear survival value. Our hypothesis was that adaptation to high-plant density is a component of yield potential and therefore amenable to genetic dissection. Plants subject to high density tend to reduce the number of grains set, but genotypes better adapted to the "density stress" show less reduction in the number of grains per spike. Therefore, the objectives of the present study were twofold: (1) to quantify the effects of plant density on grain yield, thousand kernel weight, and grain number, and (2) to identify genomic regions for adaptation to plant density in the wheat association mapping initiative (WAMI) panel through a genome-wide association study (GWAS).

Summary of Results

Adaptation to agronomic plant density is a component of high-yield potential important in crop breeding. Earlier studies have shown that progress in genetic yield potential is associated with adaptation to agronomic planting density. In the current study, a wheat association mapping initiative (WAMI) panel of 287 elite lines was assessed for the effects of plant density on grain yield (YLD), thousand kernel weight (TKW), and grain number (GNO); measured on each line of the population planted in four rows. Results of comparing YLD and GNO of two inner (high plant density) rows with two outer rows (low plant density) in each bed indicated a consistent pattern: genotypes that performed best under intense competition (inner rows) responded less to reduced competition (outer rows) while being generally the best performers on aggregate whole plot (inner + outer). TKW was not affected by plant density (**Fig. 1**).

Performance of Inner and Outer Rows in the Four Row Plots

On average, inner rows yielded 37 % less than outer rows, and the yield of inner rows ranged from 40 to 90% of the yield of outer rows. Inner rows had 37 % lesser GNO, with a range of 41 to 88% of outer rows. For TKW, the percentage differences between inner and outer rows ranged from -9% to 5%, indicating that TKW was higher in some inner rows by 9%, and in some cases that outer rows had higher TKW by 5%. On average the inner rows had 1% higher TKW than outer rows, that is not significant. To give a reference point for YLD and GNO in conventional units, values for I+O were calculated on an area basis. YLD per bed (I+O) had a range of 4.2- 8.4 t ha^{-1}, with an average 6.8 t ha^{-1} (**Table 1**).
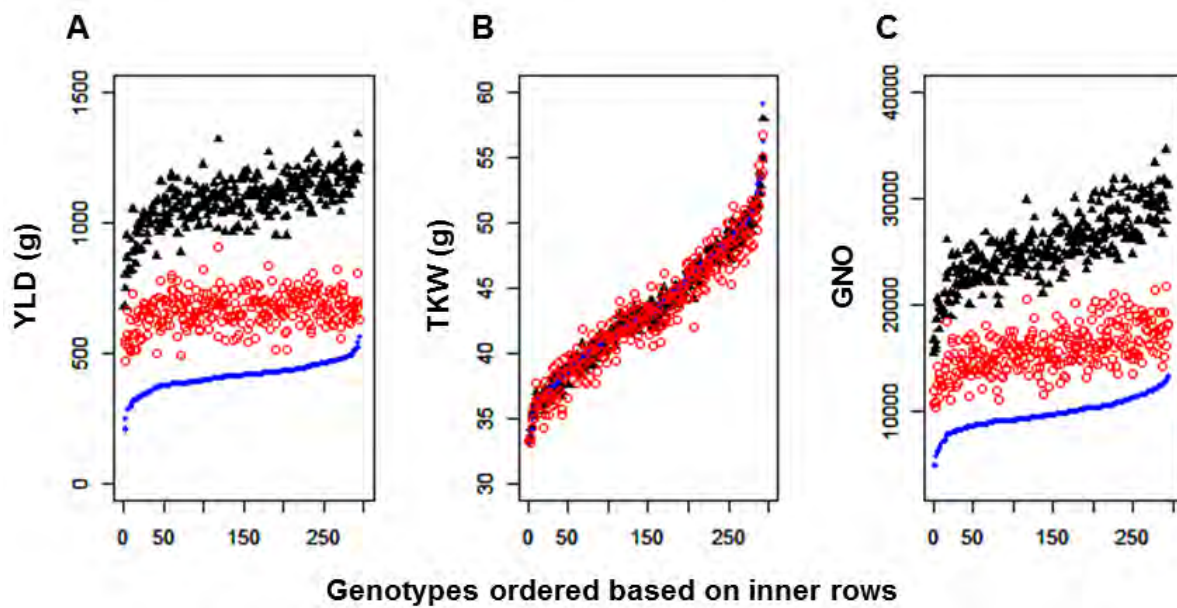
Figure 1. Comparison of (A) grain yield (YLD), (B) thousand kernel weight (TKW), and (C) grain number (GNO) of inner rows (I, blue dots), outer rows (O, red circles), and the total (I+O, black triangle) of the rows of 287 lines of WAMI (Wheat association mapping initiative) panel grown with four rows at Cuidad Obregon, Mexico from 2009-2010 to 2011-2012. The *x*-axis (genotypes) was sorted based on the value of respective traits at inner rows. For TKW, average of inner and outer was represented by black triangle. For YLD and GNO, outer rows were higher yielding than inner rows.

Table 1. Mean and range of the traits studied in WAMI at Cd. Obregon, Mexico from 2009-2010 to 2011-2012 (3 years) under four row planting. *I* inner two rows, *O* outer two rows, *YLD* grain yield, *GNO* grain number, *TKW* thousand kernel weight, *SD* standard deviation

	YLD (g m^{-1})		YLD (g m^{-2})		GNO m^{-1}		GNO m^{-2}		TKW (g)	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
I	104.0 ±12.6	52.1-141.4	260.1 ±31.5	130.2-353.5	2424 ±358	1197-3312	6060 ±896	2993-8280	43.5 ±4.6	33.3-59.1
O	167.2 ±16.7	117.8-227.1	418.1 ±41.6	294.4-567.8	3923 ±527	2558-5437	9808 ±1318	6396-13593	43.1 ±4.6	33.2-56.7
I + O	271.35 ±24.1	169.9-334.9	678.1 ±60.3	424.7-837.1	6347 ±796	3857-8644	15868 ±1990	9643-21610	43.1 ±4.5	33.3-57.5

Adaptation to Density Index (ADi) and its Association with High Yield

To identify the genetic loci for *ADi* and to know *ADi*'s association with high yielding sites, *ADi* was computed as the scaled difference in trait values between inner and outer rows. We calculated *ADi* for grain yield and grain number as:

$$ADi = (YLD_O - YLD_I) \times \frac{\mu}{\mu l}$$

where *ADi* is adaptation to density index, *YLD*o is the grain yield of outer rows and YLD_I is the grain yield of inner rows , μ is the grand mean of all data gathered over three years, and μl is the mean of the specific trial. In addition WAMI was also evaluated at 33 international sites (Mexico, Iran, Sudan, Egypt, Nepal, India, and Bangladesh, and Pakistan) under two rows per bed system and grain yield was recorded in 2010 and 2011 (Lopes et al. 2012). We used the data to evaluate the hypothesis that adaptation to density index (*ADi*) is a component of high-yield potential in wheat. Results of correlation biplot analysis indicated that *ADi* is correlated with grain yield in high yielding environments; suggesting it is a component of high yield potential (**Figure 2**).

6

Figure 2. Biplot of adaptation to density index (*ADi*) with the yield of international sites in 2010, 2011, and 2012.
Biplot indicates that adaptation to density index (*ADi*$_{YLD}$) is correlated with the grain yield in high-yielding environments. Environments with high yield are shown in blue and low-yielding environments in black. *ADi* for each year (*ADi*_10, 11, and 12) and combined three years (*ADI*$_{YLD}$) are shown in red. Dotted lines indicate the maximum number of locations with high yield. WAMI grown in international environments are abbreviated to reflect their environment (*Ban* Bangladesh, *Ir_A* Iran Ahwaz, *Nep* Nepal, *Su_W* Sudan Wadmed, *In_Dh* India Dharwad, *Pak* Pakistan, *In_V* India Varanasi, *Me_HD* Mexico heat and drought, *Me_D* Mexico drought, *Ind_D* India Delhi, *Me_H* Mexico heat, *Su_D* Sudan Dongola, *In_K* India Karnal, *Su_H* Sudan Hudeiba, *Ir* Iran Darab, *In_I* India Indore, *In_L* India Ludhiana, *Eg_S* Egypt Souhag, *Eg_E* Egypt El Mat, and *Me_YP* Mexico yield potential) followed by the year 2010 or 2011.

Molecular Markers for Adaptation to Density Index through GWAS

Genotyping of the WAMI panel was done through 90K Illumina Bead SNPs array. Association mapping employed using 18,104 SNPs markers for *ADi* identified a major locus in chromosome 3B at 71cM that explained 11.4% variation in *ADi* for YLD and GNO (**Figure 3**). The marker *IAAV7721* in chromosome 3B was further analyzed through BLAST search in National Center for Biotechnology Information (NCBI) and it resulted in a BLAST hit of *SET domain protein gene* with 99% identity. SET domain proteins are associated with pollen abortion in *Arabidopsis* (Xu et al. 2010). This marker was also identified for grain yield in our recent study, often the case for yield and yield components (Sukumaran et al. 2015).
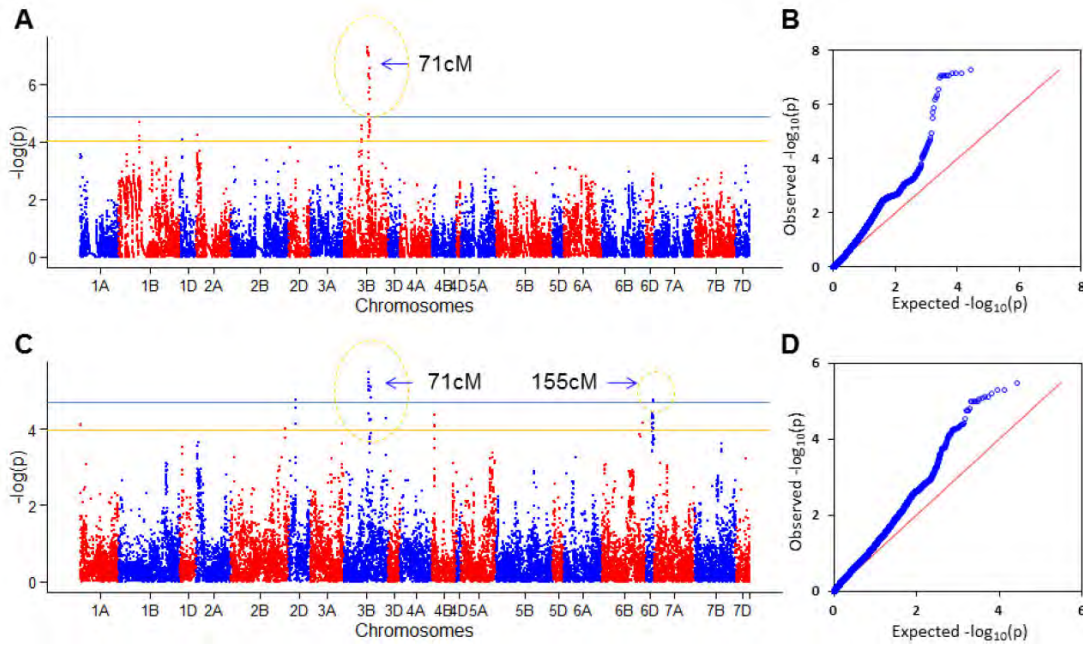
Figure 3. Manhattan plots (A and C) and *quantile-quantile* (Q-Q) plots (B and D) of the GWAS results for adaptation to density index for yield (ADi_{YLD}) and for grain number (ADi_{GNO}), respectively with the best model (*PC10+K*). The threshold was taken as $-\log_{10}(p) < 10^{-04\ \text{and}\ 05}$. Significant loci above $-\log_{10}(p) < 10^{-05}$ are illustrated with circles and marker position with lowest *p*-value is noted.

GWAS results for the adaptation to density index are shown in **Table 2**. The marker on 3B was also identified for ADi_{GNO}. Also markers on 1B, 2A, 2D, 3B, 4B, and 6B were associated with the density index that explained 6 to 8 % variation for the trait and with *p*-values lower than 1.76×10^{-05}.

Table 2. GWAS results for adaptation to density for yield (ADi_{YLD}) and grain number (ADi_{GNO}) in the WAMI population.

Trait	Marker	Alleles	Chr.	Position (cM)	*P*-value Best model	Marker R^2
ADi_{YLD}	*IAAV7721*	A (35)/G (242)	3B	71.34	6.98×10^{-08}	11.04
	wsnp_BE443531B_Ta_1_1	C (277)/T (33)	1B	64.31	2.18×10^{-05}	7.12
	BS00022393_51	C (250)/T (32)	2A	25.97	5.63×10^{-05}	5.89
ADi_{GNO}	*IAAV7721*	A (35)/G (242)	3B	71.34	5.19×10^{-06}	7.63
	RAC875_c3156_630	C (194)/T (73)	6D	155.55	1.81×10^{-08}	6.80
	D_GB5Y7FA01EHPZX_186	C (159)/T (105)	2D	50.82	1.76×10^{-05}	7.12
	Tdurum_contig76213_958	C (145)/T (119)	4B	38.06	4.30×10^{-05}	6.60
	Kukri_rep_c68091_971	C (202)/T (77)	6B	118.99	6.85×10^{-05}	5.76

Chr Chromosome   , *MAF* minor allele frequency

Possible Hypotheses for Adaptation to Density

A number of hypotheses could be tested to explain genetic differences in adaptation to density. For example, a more optimal distribution of chlorophyll b—i.e. light antenna pigments—throughout the canopy that permits increased light penetration to lower leaves, resulting in a greater proportion of leaves operating close to optimal light levels, and therefore increased radiation use efficiency (RUE) (Melis 2009; Ort et al. 2011). Another hypothesis, more difficult to test, is that high plant density—perhaps in response to red/far red light receptors or other responses induced by a "density" stress—elicits a plant growth regulator response reducing grain set (Ugarte et al. 2010; Blum 2013). Spikes m^{-2} were higher in the adapted lines than the non-adapted lines (Reynolds et al. 1994). A third hypothesis would be that lines adapted to density express a tiller dynamic whereby their production and abortion is somehow minimized or optimized.

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Evaluation of the WYCYT in Five Irrigated Wheat-Growing Locations in Mexico

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Background

Wheat is grown in Mexico mainly under irrigation in the northwestern and central regions of the country. Mexico bridges a range of latitudes, providing an array of topography, environments, soil types and epidemiological zones susceptible to different diseases. These characteristics offer important information about the performance and adaptability of outstanding wheat lines that eventually may be the basis for the development and international release of high-yielding varieties through the Wheat Yield Consortium (WYC). The evaluated material is listed in Table 1, and the location of the nurseries (environments, E) is shown in Figure 1. Data were recorded for: 1) Plant height (PH); 2) days to heading (DH); 3) days to maturity (DM); 4) harvest index (HI); 5) grain yield (GY); 6) biomass (BIO); 7) spikes per square meter (SSM); 8), thousand kernel weight (TKW); and 9) grains per square meter (GSM). HI, BIO and SSM were not considered for Obregon. Data obtained for all recorded variables were subjected to an analysis of variance within each site. Additionally, combined analyses of variance were performed over various locations and regions (northwestern and central) to estimate the statistical significance of effects due to genotypes (G), E and the genotype by environment (GxE) interaction. The AMMI1 programming routine described by Vargas and Crossa (2000) was employed to explain the GxE interaction estimated by the combined analysis of variance.

Summary of Results

At least significant differences ($p < 0.05$) in PH among genotypes were detected in all locations: in DH, in all locations, except Baja California (BC); in DM, only in Sinaloa (Sin) and Sonora (Son); in HI, only in Guanajuato (Gto) and Jalisco (Jal); in GY, only in Jal and Son; in Bio, only in Jalisco; in SSM, only in BC and Jal; in TKW, in all locations, and in GSM, in Jal and Sin. About PH, DH, DM, GY and TKW, evaluated in all the locations, combined analysis detected highly significant differences ($p < 0.01$) among E and at least significant differences ($p < 0.05$) among G; at least significant differences in GxE interactions were detected for PH, DH, DM and TKW. For HI, BIO, SSM and GSM, evaluated in 4 locations, highly significant differences were detected among E and among G; GxE interactions were highly significant for HI and SSM. Analyzing by regions, lines 41, 29 and 27 were the best for GY in Bajío (Gto and Jal), and lines 8, 20 and 7 were outstanding in the northwest (BC, Son and Sin). As a general average the most yielding line was the number 20 (BCN/WBLL1//PUB94.15.1.12/WBLL1), with 6,417 kg ha^{-1}.

Implications for Yield Potential

Average GY ranged from 6,647 kg (BC) to 5122 (Jal). Average GY for Gto, Sin and Son were 5,930, 5,239 and 5,814 kg, respectively. Although GxE interaction was not significant for GY, it is important to mention that, considering the AMMI1 approach, Jal and BC were identified as the best locations to discriminate for PH; BC for PH; Sin and Son for DM; BC and Gto for TKW; there was no a good location to discriminate for HI, although BC presented the highest values and Sin the lowest; Jal was the best location to discriminate for SSM. Recognizing that all of these parameters eventually are related to GY, it is considered important to maintain this multi-location approach to better understand their interactions.

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Table 1. Second WYCYT (Wheat Yield Consortium Yield Trial) evaluated in five locations in Mexico during 2013-2014.

Genotype No.	Genealogy
1	WEEBILL1
2	ROELFS F2007
3	BAV92/ROLF07
4	BAV92/ROLF07
5	BCN/WBLL1//ROLF07
6	BCN/WBLL1//ROLF07
7	WBLL1//YANGLING SHAANXI/ESDA/3/ROLF07
8	WBLL1//YANGLING SHAANXI/ESDA/3/ROLF07
9	WBLL1//YANGLING SHAANXI/ESDA/3/ROLF07
10	CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO/7/ROLF07
11	HE1/2*CNO79//BAV92/3/ROLF07
12	HE1/2*CNO79//BAV92/3/ROLF07
13	BCN/WBLL1
14	WBLL1//PUB94.15.1.12/WBLL1
15	WBLL1//PUB94.15.1.12/WBLL1
16	WBLL1//PUB94.15.1.12/WBLL1
17	SERI/BAV92//PUB94.15.1.12/WBLL1
18	SERI/BAV92//PUB94.15.1.12/WBLL1
19	SERI/BAV92//PUB94.15.1.12/WBLL1
20	BCN/WBLL1//PUB94.15.1.12/WBLL1
21	BCN/WBLL1//PUB94.15.1.12/WBLL1
22	BCN/WBLL1//PUB94.15.1.12/WBLL1
23	SOKOLL/4/C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH
24	SOKOLL//PUB94.15.1.12/WBLL1
25	SOKOLL//PUB94.15.1.12/WBLL1
26	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF
27	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF
28	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF
29	SOKOLL
30	PASTOR//HXL7573/2*BAU/3/WBLL1
31	PASTOR//HXL7573/2*BAU/3/WBLL1
32	PASTOR//HXL7573/2*BAU/3/WBLL1
33	PASTOR//HXL7573/2*BAU/3/WBLL1
34	PASTOR//HXL7573/2*BAU/3/WBLL1
35	PASTOR//HXL7573/2*BAU/3/WBLL1
36	PASTOR//HXL7573/2*BAU/3/WBLL1
37	SOKOLL/WBLL1
38	BCN/WBLL1
39	WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBLL1
40	D67.2/PARANA 66.270//AE.SQUARROSA (320)/3/CUNNINGHAM
41	QUAIU
42	TACUPETO F2001

Figure 1. Location of Wheat Yield Consortium Trials in Mexico, during 2013-2014 season.

Evaluation of the Stress Adaptive Trait Yield Nursery (SATYN) in Irrigated Wheat Growing Locations in Mexico

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Background

Wheat is grown in a wide variety of environments, ranging from fully irrigated (e.g. northern India and Egypt), high precipitation (e.g. northwestern Europe, east Africa, southern part of Latin America) and drought-prone (e.g. US Great Plains, most of Australia and parts of Argentina) regions. In these areas wheat production undergoes a series of biotic and abiotic factors and crop improvement requires a precise approach of the needs of crops in each zone, by producers, the processing industry and consumers (Lantican et al., 2002). In Mexico, for example, wheat is grown in nearly every state, although its cultivation is limited by temperature, with the optimum ranging between 10 and 25 ° C (Aguilar, 1991). Wheat breeding worldwide has been of great impact as this cereal has spread to most favorable climates for agriculture, through the development of varieties adapted from tropical climates to the semi-desert or in environments that are located from sea level up to just over 3000 m (Villaseñor et al., 2004). To date, traditional selective breeding has been the main force behind wheat yield; however, "the records suggest that the advances will not be quick enough to overcome the complex challenges of population growth and climate change. In spite of predicted increases in demand for wheat at a rate of around 1.6% p.a. until 2050 (Rosegrant and Agcaoili 2010), productivity in farmers' fields is increasing globally at only 1.1% p.a. (Dixon et al. 2009), and stagnating in some regions (Brisson et al. 2010), and it has been suggested that a direct solution to these problems will be to increase productivity on currently cultivated land through adoption of cultivars with improved genetic yield potential which is related to farm level yields (Fischer and Edmeades 2010) and expressed under a broad range of conditions (Reynolds et al. 2009)", Reynolds and Braun, 2013. Therefore, as part of this initiative, the National Institute for Forestry, Agriculture and Livestock (INIFAP) collaborates with the International Maize and Wheat Improvement Center (CIMMYT) evaluating elite genotypes in different regions in Mexico with the aim of identifying those outstanding in grain yield and biomass.

Summary of Results

This document provides the analysis of information for the SATYN Experiment set in five locations in the Bajio and northwest wheat producing regions of Mexico during the 2013-14 wheat growing cycle. Sites of evaluation were located in the states Guanajuato, Jalisco, Sonora, Sinaloa and Baja California. Twenty four (24) bread wheat entries OR GENOTYPES were evaluated and data recorded for: 1) Plant height (PH), 2) days to heading (DH), 3) days to maturity (DM), 4) harvest index (HI), 5) grain yield (GY), 6) biomass (BIO), 7) spikes per square meter (SSM), 8), Weight of 1000 grains (TGW) and 9) grains per square meter (GSM). Days to maturity where not considered for Jalisco and HI, BIO and SSM for Sonora. Data obtained for all recorded variables were subjected to an analysis of variance within each site and combined analyses of variance were performed over locations to estimate the statistical significance of effects due to genotypes, locations and the genotype by environment interaction. The AMMI1 programming routine described by Vargas and Crossa (2000) was employed to explain the genotype by environment interaction estimated by the combined analysis of variance for grain yield.

Mean square estimates due to genotypes for measured traits at each location not shown here detected statistically significant differences among genotypes for GY, DH and DM in all locations. Statistically significant differences were also detected among genotypes for PH, BIO, SSM and GSM in at least three locations. Harvest index and thousand-grain weight, respectively, only showed statistically significant differences in Jalisco and Baja California.

The combined analyses of variance for variables showing statistical significance for all sources of variation of interest are presented in Table 1. Effects to due locations and genotypes showed a high statistical significance ($p \leq 0.01$) for days to heading, days to maturity, grain yield, biomass, spikes per square meter and grains per square meter. With the exception of days to heading which showed a $p \leq 0.05$ statistical significance, the genotype by environment interaction showed a high ($p \leq 0.01$) for the rest of the variables.

Table 1. Combined analysis of variance over locations for variables recorded from the Stress Adaptive Yield Nursery evaluated in Mexico during the 2013-2014 wheat-growing cycle.

S of V	DH	DM	GY	BIO	SSM	GSM
LOC	6035.0**	3481.57465**	26264734.0**	134.6**	409174.3**	212380622.5**
REP (LOC)	1.7	2.80729	998587	2.2	1286.9	4282899
GEN	46.2**	34.90014**	4704949.5**	18.3**	33097.6**	27843767.2**
GEN*LOC	7.5*	9.00581**	837550.0**	5.5**	5397.2**	5137873.7**
ERROR	2.1	2.31816	445020.4	3.2	2831	2482752
C.V	1.8	1.226164	12.47	15.1	16.4	13.3
AVERAGE	79.9	124.1719	5347.9	11.8	323.7	11766.9

S of V = Source of variation; PH = Plant height; DH = Days to heading; DM = Days to maturity; HI = Harvest index; GY = Grain yield; BIO = Biomass; SSM = Spikes per square meter; TGW = thousand-grain weight; GSM = Grain per square meter; LOC = Location, GEN = Genotype; GEN*LOC = Genotype by location interaction.

Besides showing the highest average value for grain yield, 6,307 kg ha^{-1}, greatest average values for DH (92 days) and TGW (52 g) were observed in Baja California (Table 2). Highest values for PH (104 cm), DM (135 days) and BIO (13.4 t ha^{-1}) and GSM (14,263) were observed in Guanajuato; while Jalisco showed the highest values for HI (0.53) and SSM (456), Table 2. On the other hand, Sinaloa showed lowest values for GY (4,449 kg ha-1), DM (114 days), HI (0.53), SSM (251) and GSM (9,310), followed by Jalisco where lowest values were observed for PH (83 cm), DH (66 days) and BIO (9.5 t ha^{-1}), while Guanajuato only recorded the lowest value for TGW (42 g).

Table 2. Estimated means for nine variables averaged over 24 genotypes grown in five locations during the 2013-14 wheat cycle in Mexico.

Location	PH	DH	DM	GY	TGW	HI	BIO	SSM	GSM
Baja California	84	92	123	6,307	52	0.51	12.5	318	12,457
Guanajuato	104	88	135	5,875	42	0.44	13.4	270	14,263
Sonora	96	84	125	5,126	47				11,037
Jalisco	83	66		4,983	46	0.53	9.5	456	11,038
Sinaloa	94	70	114	4,449	48	0.39	11.6	251	9,310

PH = Plant height; DH = Days to heading; DM = Days to maturity; HI = Harvest index; GY = Grain yield; BIO = Biomass; SSM = Spikes per square meter; SSM = Grains per square meter.

Average over locations for genotypes ranged from 3,010 to 6121 kg ha^{-1} for GY; 83 to 101 cm for PH, 77 to 84 days for DH, 121 to 129 days for DM, 39 to 55 g for TGW, 7.2 to 12.7 t ha^{-1} for BIO, 176 to 451 for SSM and 7,117 to 15,014 for GSM, Table 3.

Correlation coefficients estimated using phenotypic means calculated over locations involving grain yield only showed a closer and positive relationship with biomass (r=0.95) followed by those with SSM (r=0.77), GSM (r=0.76) and PH (r=0.50).

The AMMI1 programming routine employed to explain the genotype by environment interaction showed that environments, genotypes and their interaction explained 30.3, 31.2 and 22.2% of the sum of total sum of squares for grain yield in the model, while the first two components of AMMI analysis explained 65.9% of the variation due to the genotype by environment interaction. A graphical representation (biplot graph) of genotypes and environments is presented in Figure 1. On the x-axis grain yield for genotypes and environments is depicted, and on the y-axis stability is measured; that is, values closer to zero are considered stable while those distant from the principal component one (PCA1) are considered unstable. The dotted line perpendicular to the x-axis indicates the average yield of genotypes, so that the genotypes and environments plotted to the left of the x-axis are the lower grain yielding genotypes and environments, while on the right side of the x-axis genotypes and environments showing a higher performance are located.

It can be observed in Figure 1 that genotypes 9424, 9402 and 9403 display the highest performance; while genotypes 9412, 9415 and 9410 showed the lowest yields. The Baja California site exhibited the highest grain yields followed by Guanajuato, with both recording above average yields. Sonora, Jalisco and Sinaloa sites show below average yields.

Table 3. Estimated of highest and lowest mean values for eight variables in genotypes evaluated in the Stress Adaptive Yield Nursery sown in Mexico during the 2013-2014 wheat-growing cycle.

Genotype	PH	DH	DM	GY	TGW	BIO	SSM	GSM
9424	94	78	123	6,121	45	12.7	371	13,923
9402	95	79	122	6,033	55	13.0	307	11,196
9403	101	80	125	6,012	50	12.7	326	12,192
9406	84	77	121	5,849	44	12.1	408	13,744
9422	98	81	125	5,756	47	13.1	360	12,177
9405	96	77	123	5,663	39	12.8	451	15,014
9411	93	84	128	5,130	39	11.0	309	12,838
9412	83	83	129	3,010	46	7.2	176	7,117

PH = Plant height; DH = Days to heading; DM = Days to maturity; GY = Grain yield; TGW = Thousand grain weight, BIO = Biomass; SSM = Spikes per square meter; SSM = Grains per square meter.
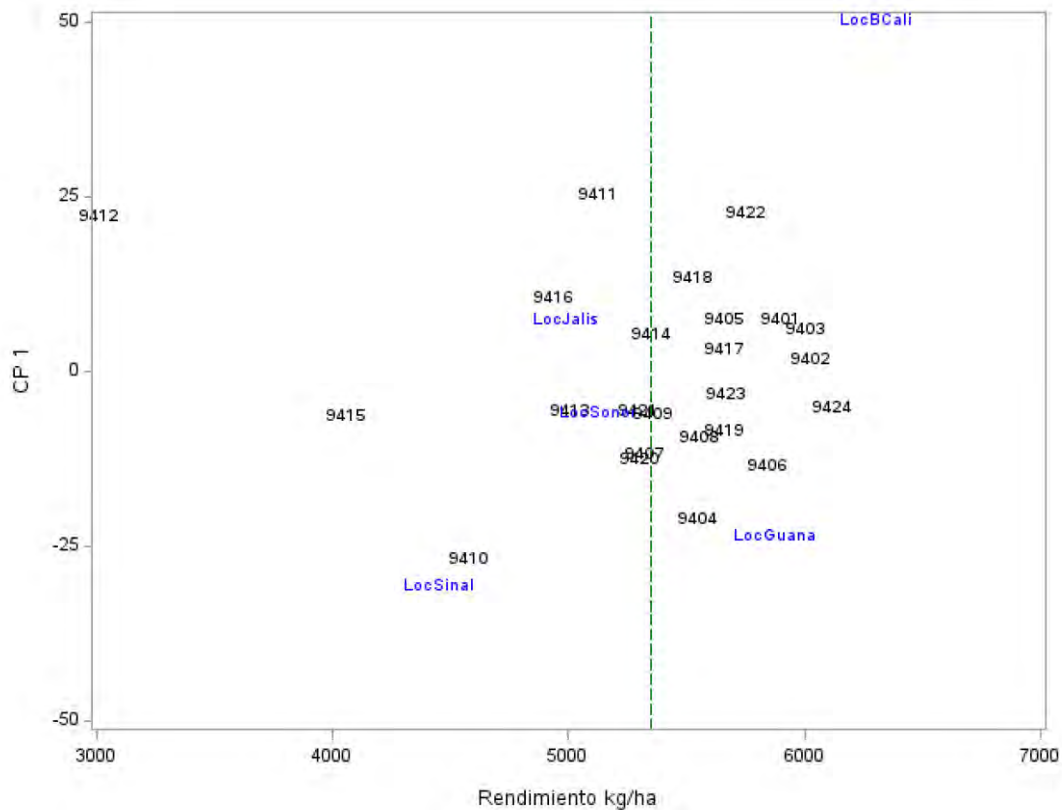
Genotypes showing PCA1 values greater than zero are well suited to environments that similarly have values of PCA1> 0; genotypes and environments interact positively, but respond negatively in environments that have values of PCA1 <0. The opposite applies for genotypes that have values of PCA1 <0 (Samonte et al., 2005). Jalisco and Sonora displayed lower PCA1 values, i.e., they were the most stable; therefore, these environments discriminate genotypes to a lesser extent since most of them had similar responses. Instead, Baja California is the best to discriminate genotypes. Genotypes 9402 and 9424 were notorious for their high performance and stability.

Implications for Yield Potential

Correlation analyses using the particular set of bread wheat entries included in the Stress Adaptive Trait Yield Nursery (SATYN) indicate that there is a close and positive relationship between grain yield and biomass, spikes per square meter, grains per square meter and plant height. These relationships show a considerable opportunity for improving grain yield and its direct components, spikes and grains per square meter, by jointly increasing biomass and plant height. However, a limit to avoid lodging might have to be set for plant height, mainly in irrigated wheat-growing areas having poor-structured soils, like those in northwest Mexico, where levels of organic matter are very low.

Genotype by environment interaction continues challenging plant breeders and agronomists who drive crop performance trials over different environments, and can reduce progress from selection. Stability of performance has to be considered an important aspect of yield trials. Although inferences extracted from biplots are valid only when the first PCA or the first two explain maximum variation due to interaction, the AMMI analysis offers the possibility of selecting for yield and stability.

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Pre-Breeding for Yield Potential: Summary of International Data from 2nd WYCYT and Performance of Pipeline Material

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Background

In order to accelerate genetic gains from their current rate of around 0.6% p.a. (Sharma et al. 2012), given that genetic bases of cultivar level differences in yield potential is still largely unknown, wheat breeding efforts currently depend on three main approaches: 1) Strategic hybridization to combine complementary yield potential traits; 2) Use of exotic germplasm to complement levels of expression in conventional gene pools; 3) High throughput phenotyping for progeny selection. Using all information available on photosynthetic and partitioning traits, hybridization schemes were designed to combine physiological traits (PTs) with the view to achieving cumulative gene action for yield potential (Reynolds et al. 2012). These approaches have recently delivered new germplasm that expressed both higher yield and biomass compared to local checks at the majority of the 18 international sites where they were tested, as the 1st International Wheat Yield Consortium Yield Trial (1st WYCYT) in 2013 (see Reynolds et al. 2014). Progeny from this breeding effort and other material developed using similar approaches are already being used to better understand the genetic basis of yield potential (e.g. Griffiths et al. 2015). The pre-breeding effort is ongoing, and the following data result from subsequent international yield trials and germplasm evaluations in Mexico.

Summary of Results

The 2nd WYCYT consisted of 35 new PT lines, seven elite CIMMYT checks (Table 1) and was grown at 26 international sites in 2014 (Table 2), for which performance data is summarized (Table 3). In addition, this report presents information on candidates for the 3rd WYCYT that were tested in Obregon in 2014 for international distribution later this year (Table 4). It also discusses primary re-synthesized hexaploid lines expressing promising yield potential characteristics (Figure 1) that are candidates for new crosses.

Research showed that new PT lines were the best, yielding at 23 out of 26 sites by an average of 10% over the best CIMMYT check at that site, and by as much as 20% (Table 3). When considering all new PT lines, average yield at each site showed superior performance compared to the average yield of all checks at all sites by an average of 7%, and up to 18% at the best site. A PT line (with the pedigree SERI/BAV92//PUB94.15.1.12/WBLL1) expressed the highest average yield across all sites.

Above ground biomass was reported for 13 sites and PT lines expressed the highest biomass at all 13 sites, by on average 14% above the best CIMMYT check and by up to 25% at the best site. When considering all new PT lines, their average biomass at each site was higher than the average biomass of all checks, again at all sites, by on average 6%, and up to 12% at the best site.

Across all sites, the new PT material was on average one day earlier to anthesis than the average of all checks, expressed the same number of days to maturity, and was on average 2% taller (2cm).

Table 1. Main effect of agronomic trait expression across 26 environments for lines of the 2nd Wheat Yield Consortium Yield Trial (WYCYT).

	CROSS NAME	SELECTION HITORIC	YIELD (g/m^2)	Biomass (g/m^2)	Heading (d)	Maturity (d)	Height (cm)
New PT	SERI/BAV92//PUB94.15.1.12/WBLL1	PTSS09GHB00019S-0SHB-099Y-099B	531	1223	88.7	122	95.2
CIMMYT Check	QUAIU	CGSS01B00046T-099Y-099M-099M-099Y-099M-10WGY-0B	512	1252	86.4	120	96.5
New PT	BCN/WBLL1//PUB94.15.1.12/ WBLL1	PTSS09GHB00024S-0SHB-099Y-099B	504	1264	87.8	121	93.0
New PT	WBLL1//YANGLING SHAANXI/ESDA/3/ROLF07	PTSS07GHB00008S-0GHB-0Y-099B-1Y-0Y	504	1257	85.4	121	95.1
New PT	BCN/WBLL1//PUB94.15.1.12/ WBLL1	PTSS09GHB00024S-0SHB-099Y-099B	503	1254	88.3	122	96.4
New PT	SERI/BAV92//PUB94.15.1.12/WBLL1	PTSS09GHB00019S-0SHB-099Y-099B	502	1237	88.3	122	94.9
New PT	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF	PTSS09GHB00057S-0SHB-099Y-099B	501	1268	87.1	122	97.7
New PT	SOKOLL/WBLL1	PTSS02Y00021S-099B-099Y-099B-099Y-213B-0Y	498	1314	88.4	121	96.3
New PT	WBLL1//YANGLING SHAANXI/ESDA/3/ROLF07	PTSS07GHB00008S-0GHB-0Y-099B-1Y-0Y	497	1253	85.3	121	96.4
New PT	WBLL1//PUB94.15.1.12/WBLL	PTSS09GHB00009S-0SHB-099Y-099B	495	1236	89.1	123	95.6
New PT	HE1/2*CNO79//BAV92/3/ROLF07	PTSS07GHB00014S-0B-0Y-099B-7Y-0Y	495	1280	84.9	120	95.6
New PT	PASTOR//HXL7573/2*BAU/3/WBLL1	PTSS02Y00023S-099B-099Y-099B-099Y-5B-0Y	495	1190	87.6	121	94.8
CIMMYT Check	SOKOLL	CMSS97M00316S-0P20M-0P20Y-51M-010Y-0Y	494	1151	85.8	120	94.1
New PT	SOKOLL//PUB94.15.1.12/WBLL1	PTSS09GHB00044S-0SHB-099Y-099B	493	1198	86.8	122	97.2
New PT	BCN/WBLL1//ROLF07	PTSS07GHB00006S-0GHB-0Y-099B-6Y-0Y	489	1225	86.2	121	92.9
New PT	PASTOR//HXL7573/2*BAU/3/WBLL1	PTSS02Y00023S-099B-099Y-099B-099Y-75B-0Y	488	1131	87.2	121	97.0
New PT	BCN/WBLL1//ROLF07	PTSS07GHB00006S-0GHB-0Y-099B-1Y-0Y	488	1229	86.3	122	94.1
New PT	SOKOLL//PUB94.15.1.12/WBLL1	PTSS09GHB00044S-0SHB-099Y-099B	487	1270	88.8	122	95.9
New PT	WBLL1//PUB94.15.1.12/WBLL	PTSS09GHB00009S-0SHB-099Y-099B	486	1249	87.6	122	96.6
New PT	CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO/7/ROLF07	PTSS07GHB00010S-0GHB-0Y-099B-9Y-0Y	483	1194	85.3	120	94.1
New PT	PASTOR//HXL7573/2*BAU/3/WBLL1	PTSS02Y00023S-099B-099Y-099B-099Y-134B-0Y	483	1084	85.3	120	93.1
CIMMYT Check	ROELFS F2007	CGSS00B00169T-099TOPY-099M-099Y-099M-9CEL-0B	483	1173	85.5	119	92.5
New PT	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF	PTSS09GHB00057S-0SHB-099Y-099B	483	1137	85.1	120	98.0
New PT	BCN/WBLL1	PTSS02GH00001S-0Y-0B-040M-040Y-9M-0Y-0Y-0Y	482	1212	87.1	121	95.7
New PT	WBLL1//YANGLING SHAANXI/ESDA/3/ROLF07	PTSS07GHB00008S-0GHB-0Y-099B-21Y-0Y	480	1176	86.1	121	95.2
New PT	WBLL1//PUB94.15.1.12/WBLL	PTSS09GHB00009S-0SHB-099Y-099B	480	1231	88.7	122	96.8
New PT	BAV92/ROLF07	PTSS07GHB00005S-0GHB-0Y-099B-18Y-0Y	480	1202	84.8	119	91.3
CIMMYT Check	TACUPETO F2001	CGSS95B00016F-099Y-099B-099Y-099B-15Y-0B-0MEX	479	1268	86.3	119	95.3
New PT	BCN/WBLL1//PUB94.15.1.12/ WBLL1	PTSS09GHB00024S-0SHB-099Y-099B	479	1223	89.5	123	93.6
New PT	PASTOR//HXL7573/2*BAU/3/WBLL1	PTSS02Y00023S-099B-099Y-099B-099Y-35B-0Y	474	1135	85.5	120	95.8
New PT	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF	PTSS09GHB00057S-0SHB-099Y-099B	471	1168	86.9	121	96.4
New PT	SERI/BAV92//PUB94.15.1.12/WBLL1	PTSS09GHB00019S-0SHB-099Y-099B	470	1207	87.0	121	95.4
New PT	SOKOLL/4/C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH	PTSS09GHB00041S-0SHB-099Y-099B	469	1173	85.4	122	100.1
New PT	HE1/2*CNO79//BAV92/3/ROLF07	PTSS07GHB00014S-0B-0Y-099B-3Y-0Y	469	1144	84.8	120	97.2
New PT	PASTOR//HXL7573/2*BAU/3/WBLL1	PTSS02Y00023S-099B-099Y-099B-099Y-56B-0Y	469	1106	84.9	120	96.1
New PT	BAV92/ROLF07	PTSS07GHB00005S-0GHB-0Y-099B-18Y-0Y	468	1137	85.0	121	91.8
New PT	BCN/WBLL1	PTSS02GH00001S-0B-0Y-0B-23Y-0B-0Y-0Y-0Y	460	1111	87.2	122	92.0
New PT	PASTOR//HXL7573/2*BAU/3/WBLL1	PTSS02Y00023S-099B-099Y-099B-099Y-180B-0Y	451	1112	87.8	121	96.1
New PT	PASTOR//HXL7573/2*BAU/3/WBLL1	PTSS02Y00023S-099B-099Y-099B-099Y-173B-0Y	447	1090	85.6	121	94.3
CIMMYT Check	WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBLL1	CGSS03B00080T-099Y-099M-099Y-099M-33WGY-0B	434	1096	87.3	123	93.9
CIMMYT Check	WEEBILL1	CGSS95B00014T-099Y-099B-099Y-099B-35Y-0B-0B	427	1065	86.9	120	88.3
CIMMYT Check	D67.2/PARANA 66.270//AE.SQUARROSA (320)/3/CUNNINGHAM	CMSS99M02230S-040M-040SY-6M-3Y-0M-0Y-0Y-0Y-0Y	352	934	93.1	127	94.1
Mean			**479**	**1185**	**86.8**	**121**	**95.0**
CV			10.9	12.7	1.7	1.3	3.8
P>F (ENV)			0.00	0.00	0.00	0.00	0.00
P>F (ENT)			0.00	0.00	0.00	0.00	0.00
P>F (ENV*ENT)			0.00	0.00	0.00	0.00	0.00
LSD ENT (5%)			19.7	83.2	0.7	0.9	1.5
LSD ENV (5%)			15.4	44.4	0.4	0.5	1.1

Table 2. Sites returning data from 2nd WYCYT

Abbreviation	Site	Country
BGLD J	BARI Joydebpur	Bangladesh
BGLD D	BARI Dinjpur	Bangladesh
BGLD R	BARI Rajshahi	Bangladesh
China L	LAOMANCHENG	China
Egypt A	Assiut	Egypt
India D	Delhi	India
India L	Ludhiana	India
India V	Varanasi	India
India K	Karnal	India
India H	Dharwad	India
India I	Indore	India
India U	Ugar	India
Iran D	DARAB-HASSAN-ABAD	Iran
Iran Z	ZARGAN	Iran
Iran SP	SPII - KARAJ	Iran
Iran S	SAFIABAD AGRIC. RES. CENTER	Iran
MEX Bajio	INIFAP-Bajio	Mexico
MEX CM	CIMMYT CENEB	Mexico
MEX BC	INIFAP-Mexicali Baja California	Mexico
MEX JAL	INIFAP-Tepatitlan Jalisco	Mexico
MEX SIN	INIFAP-Valle del Fuerte, Sinaloa	Mexico
MEX SON	INIFAP_Valle del Yaqui	Mexico
Nepal B	Bhairahawa	Nepal
PAK I	Islamabad	Pakistan
PAK F	Faisalabad	Pakistan
PAK P	Pirsabak	Pakistan

Table 3. Summary of performance of new PT lines versus CIMMYT checks in the 2nd WYCYT at 26 International Sites, 2013/14 Spring Wheat Cycle

Environments (I)	BGLD D	BGLD J	BGLD R	China L	Egypt A	India D	India H	India I	India K	India L	India U	India V	Iran D	Iran S
Avg Yield Checks (gm^{-2}) (n=7)	500	388	323	633	884	680	271	359	382	561	466	326	299	558
Avg PT Yield (g/m^{-2}) (n=35)	507	391	344	702	925	705	319	394	421	570	479	345	325	598
% advantage	1.4%	0.7%	6.5%	10.9%	4.7%	3.7%	17.8%	9.8%	10.0%	1.7%	2.8%	5.8%	8.9%	7.0%
# lines outyielding best check	2	6	11	1	3	7	5	5	1	1	0	3	7	6
% advantage of best PT over best check	10%	10%	17%	1%	2%	13%	14%	10%	4%	5%	.	16%	**20%**	7%
Coefficient of variation	5.7	15.1	9.6	8.9	10.0	10.1	15.8	10.2	8.2	7.6	17.3	4.2	13.5	9.8

Environments (II)	Iran P	Iran Z	Mex Bajio	Mex CM	Mex BC	Mex JAL	Mex SIN	Mex SON	Nepal B	Pak F	Pak I	Pak P	Average
Avg Yield Checks (gm^{-2}) (n=7)	456	272	626	696	626	480	526	569	152	369	224	263	**455**
Avg PT Yield (g/m^{-2}) (n=35)	465	285	673	727	672	519	523	584	173	405	250	294	**485**
% advantage	2.1%	4.7%	7.5%	4.5%	7.5%	8.0%	-0.5%	2.5%	13.7%	9.8%	11.5%	11.9%	**7%**
# lines outyielding best check	0	9	10	13	10	0	11	6	6	4	1	2	**5**
% advantage of best PT over best check	.	10%	17%	8%	17%	.	6%	4%	15%	7%	2%	18%	**10%**
Coefficient of variation	8.9	7.3	16.8	4.6	15.1	15.3	7.8	7.3	14.3	9.5	13.1	11.5	

New material coming through the pre-breeding pipelines also showed considerable promise in Obregon, with the best yield expressed 12% above best check in preliminary yield trials of the 3rd WYCYT candidates (data not shown). This compares favorably with a value of 5% above the best check for the best new line of 2nd WYCYT in Obregon in 2013, despite substantially larger values in target environments (Table 3).

More recent crosses have emphasized the use of exotic germplasm and its impact is clearly seen. Table 4 shows a summary of the crosses that generated the best yielding progeny in Pre Preliminary Yield Trials. A total of 48 lines showed at least 5% greater yield than the best check. What is interesting about the new material is that all crosses involved landraces, and in some cases also re-synthesized hexaploid germplasm.

Table 4. Summary of candidates of 4th WYCYT showing at least 5% yield gain over best check (in augmented design yield trials), Obregon, Mexico, 2014 (landraces are shaded and synthetic derived lines in italics)

Pedigree	# sisters with at least 5% more yield than best check	% over best Check
BCN/WBLL1//PUB94.15.1.12/WBLL1	4	5-13%
CROC_1/AE.SQUARROSA (224)//OPATA/3/PUB94.15.1.12/WBLL1	2	6-7%
MEX94.27.1.20/3/*SOKOLL*//ATTILA/3*BCN/4/PUB94.15.1.12/WBLL1	17	5-12%
SERI/BAV92//PUB94.15.1.12/WBLL1	8	5-13%
SOKOLL//PUB94.15.1.12/WBLL1	4	5-9%
SUP152//PUB94.15.1.12/WBLL1	8	5-8%
WBLL1//PUB94.15.1.12/WBLL1	5	6-11%
Check *SOKOLL*		0%
Check ROELFS F2007		-7%

There is much exotic genetic diversity available for use in crossing from the recent screenings of a) landraces in the World Wheat Collection, and b) of primary re-synthesized hexaploids, under yield potential conditions in Obregon. Figure 1 shows the favorable expression of biomass of primary synthetics compared to elite checks, indicative of their high radiation use efficiency.

Implications for Yield Potential

The new PT lines were generated by crossing lines with superior expression of a number of relatively simple traits, including photosynthetic capacity (cool canopy temperature, crop growth rate/RUE, stem water soluble carbohydrates) to lines showing favorable expression of traits leading to high grain number and size (spike index, spike density, kernel number, kernel weight). The approach has proven successful in two successive years in achieving genetic gains for yield across a representative range of CIMMYT spring wheat target environments. Very similar results were also found for a trial run in parallel at most of the same international sites – the 3rd SATYN consisting of lines developed and selected for physiological traits associated with adaptation to warmer irrigated environments - where the best PT lines expressed the highest yields at 19/24 sites by an average of 7%, and a PT line expressed the highest average yield across all sites.

The International Wheat Yield Partnership (IWYP) initiative is expected to capitalize on this successful approach through research that will provide new information on yield potential traits and their genetic basis, and through development of molecular breeding methodologies to complement the successful trait-based approach. The favorable expression of yield potential traits in re-synthesized hexaploid lines is especially encouraging, given that to date our exploration of genetic resources has been only preliminary.
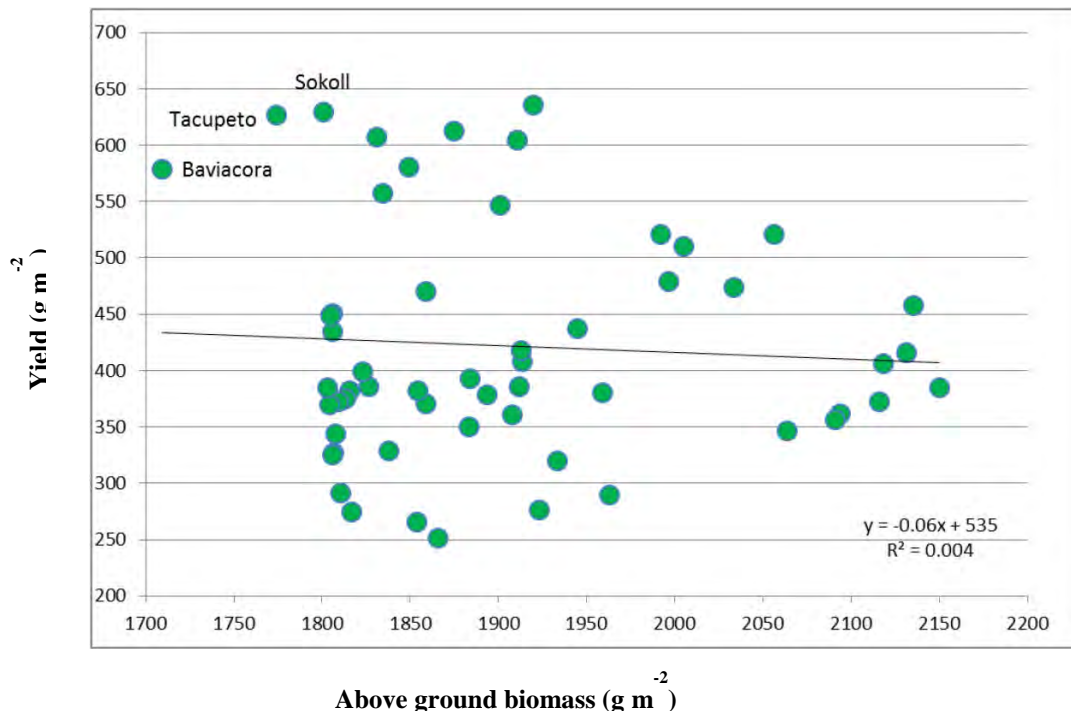
Figure 1. Lines from panel of primary synthetic hexaploids expressing high biomass characteristics, Obregon, 2014.

Now that improved yield potential and RUE has been identified in new PT lines and validated at international sites, the next step will be to refine the approach in two ways. First, the best performing new lines are being studied side-by-side with their parents in controlled field situations in order to more clearly identify and understand the contribution of respective yield potential traits and their interactions with each other and genetic background. Second, experimental progeny of the most successful crosses will be developed into mapping populations in an attempt to understand gene action for promising traits, as well as to identify candidates for gene discovery, cloning, and marker-assisted selection.

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Key traits Associated with Potential Grain Weight in Selected CIMCOG Genotypes

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Abstract

To increase grain yield potential of wheat and breeding efficiency the trade-off between grain number and kernel weight should be minimized by (i) improving the balance between the two main yield components or by (ii) increasing kernel weight potential. The aim of this study was to evaluate the trade-off between kernel weight and grain number and to assess key drivers of kernel weight potential in a selected set of 8 genotypes from the CIMCOG population. These genotypes were evaluated during the 2014/15 seasons in Valdivia (Chile) to confirm previous associations recorded in Ciudad Obregón in the light that contrasting relationships between grain yield and grain number were found in these environments. A lower trade-off between kernel weight and grain number was recorded in Valdivia where higher grain weight was reached. However, individual kernel weight showed a close association with the volume and length of grains in positions G2 and G4. In addition, kernel weight of G4 also showed association with kernel wide. Interestingly, thinning treatments augmenting the availability of resources since booting on increased both grain number and kernel weight.

Introduction

The need of increasing grain yield of wheat and the trade-off between grain number (GN) and average grain weight (TGW), reinforced by the negative relationship between these components in the CIMCOG genotypes (Wiersma et al., 2001; Sadras, 2007; Quintero et al., 2014), highlight the aim of improving TKW in breeding programs. Molecular assisted breeding in crops requires uncovering the importance of particular genes in the determination of complex traits as grain yield to improve the efficiency of plant breeding of crops for food production. Identifying the functionally linked mechanisms of yield components, i.e., grain number (GN) and average grain weight (TGW), and understanding their genetic bases, is necessary at the present to boost yield potential of wheat. From a physiological perspective, the knowledge of grain number and kernel weight determination provide important clues for a successful phenotyping and genotyping evaluation. The time-course of flowers, carpels weight, grain length and grain water content studied in the last years offer helpful trails (Ferrante et al., 2010; 2013; Calderini et al., 2001; Hasan et al., 2011). Additionally, molecular biology also delivered crucial information to build a physiological-genetic framework. Sugar signaling affecting both grain set and kernel weight (Ruan et al., 2010; Wang and Ruan, 2013), programed cell death and autophagy conditioning grain set (Ghiglione et al., 2008; Wang and Ruan, 2013), the expression of TaExpA 6 gene driving grain length (Lizana et al., 2010) and TaGW2 gene expression modifying grain wide (Bednarek et al., 2012; Simmonds et al., 2014) will be the foundations to identify promising lines by phenotyping and genotyping.

In previous evaluations of CIMCOG genotypes carried out in Ciudad Obregón, curvilinear associations were found between grain yield and GN, negative associations were identified between TKW and GN and positive relationships between TKW and grain weight of grain positions G2 were found (Quintero et al., 2014). Promising traits of individual kernel weight (IKW) were detected such as grain volume, grain length and water content of grains, which could be phenotyped in doubled haploid and RIL populations. On the hand, contrasting results were found in the CIMCOG population evaluated in a very high yielding environment like that of southern Chile where a line association between grain yield and GN was recorded. Therefore, the present study has the aim of confirming or refuting previous relationships found in C. Obregón between traits and the promising characters in the environment of southern Chile

Materials and Methods

One set of 8 contrasting genotypes in the arrangement of thousand grain weight (TKW) and grain number (GN) chosen from the 60 CIMCOG´s genotypes were assessed at the Estación Experimental Agropecuaria Austral (39˚ 47' 18"S, 73˚ 14' 5"O) of Universidad Austral de Chile (UACH), Valdivia, Chile, during the 2014–2015 growing season. The set was sown on 27 of August in 2014 under two thinning treatments (control and thinning rows in booting). Plots were arranged in a completely randomized design with 3 replicates. At the control treatment the genotypes were sown in plots 2.5 m long and 1.35 m wide, while in the thinning treatment plot dimensions were 3.5 m long and 1.35 m wide. Seed rate was 333 seeds per square meter in both treatments. The thinning treatment was carried out at booting to increase the availability of resources to the remaining plants. The thinning was carried out by removing all the plant of the two closer rows of plants. Additionally, the source-sink ratio was increased in 5 control and 5 thinning plants at heading and 10 days

after anthesis by halving the spikes. The plots were irrigated when necessary; weeds were periodically removed by hand and recommended doses of pesticides were used to prevent and control insects and diseases.

In the experiment the phenological stages were recorded (Zadoks et al., 1974). The timing of physiological maturity was estimated when grain growth stopped as in Hasan et al. (2011). At harvest, grain yield, GN and TKW were recorded. The individual kernel weight (IKW) and grain dimensions of grain position 2 (the second grain from the rachis: G2) and grain position 4 (the fourth grain from the rachis: G4) of two central spikelets were measured in at least 5 spikes per plot. Grain volume was calculated as in Hasan et al. (2011).

Twenty two main-shoot spikes of similar size and development were targeted at anthesis at each plot to follow grain growth. From anthesis on, two main shoot spikes were harvested 11 times (A+5, A+10, A+15, A+20, A+25, A+30, A+35, A+42, A+48, A+54 and A+60). The individual grain weight (IGW) was measured in G2 and G4. At each sampling two main-shoot spikes per plot were harvested.

Data were subjected to analysis of variance (ANOVA), and mean comparison by least significant difference procedure. Correlation analyses were also performed to assess the degree of association between variables.

Results

The nine genotypes evaluated in Valdivia in 2014-2015 reached grain yield between 600.7 and 770.8 g m^{-2} in control treatments although no differences were found (P>0.05). On the other hand, yield components ranged from 11336 to 18018 for GN and from 38.9 to 61.5 g for TKW. On the other hand, plants under the thinning treatment at booting showed grain yield from 865 to 1538 g m^{-2}. The GN and TKW at the thinning treatment ranged between 15158 and 32204 grains m^{-2}, and 47.4 to 68.6 g, respectively (Table 1). Taking into account recorded grain yield, the thinning treatment over-yielded the control from 42 to 105%. A positive relationship between grain yield and GN was found, while no association was detected between either grain yield and TKW (P>0.05) and between TGW and GN when all treatments were plotted together (Fig. 1). Interestingly, both GN and TKW were increased by the thinning treatment (Fig. 2), however, the response of GN to thinning was higher than that of TKW taking into account that GN increased 52%, while TKW only 16%, averaged across of the genotypes.

Table 1. Grain yield, TKW and GN of 8 genotypes under control and thinned plots evaluated in Valdivia (Chile) during the 2014-2015 growing season.

ENT	NAME	ORIGIN	CONTROL (SR) 2014-2015			THINNING (CR) 2014-2015		
			YLD (g/m²)	TGW (g)	#Grain/m²	YLD (g/m²)	TGW (g)	#Grain/m²
7	BACANORA T 88 (His	HIST	600.7	38.9	15667	1068.2	47.5	23611
26	KBIRD//INQALAB 91	RS	606.0	44.6	13842	923.7	47.4	20696
53	UP2338*2/4/SNI/TRA	RS	721.9	47.5	15493	1084.2	54.1	20973
9	BCN/RIALTO	EXPT POPS	749.5	41.5	18018	1495.4	50.5	32204
15	CAL/NH//H567.71/3/S	RS	609.4	54.3	11336	865.0	57.8	15158
29	MILAN/KAUZ//PRINIA	WAMI	715.3	50.7	14138	1228.1	61.6	21120
6	BABAX/LR42//BABAX	YM	749.4	56.6	13596	1538.3	68.2	23473
50	TC870344/GUI//TEM	YM	770.8	61.5	12780	1198.3	68.6	18120
Promedio			690.4	49.4	14358.6	1175.2	57.0	21919.4
Max			770.8	61.5	18017.8	1538.3	68.6	32204.4
Min			600.7	38.9	11335.6	865.0	47.4	15157.8
CV			16.1	3.0	14.3	12.7	2.7	12.5
P-value(ENT)			ns	***	***	***	***	***
LSD (0.05)			58.9	0.8	1086.6	79.3	0.8	1449.9
r(con Rendimiento)			1	0.47	0.24	1	0.40	0.71

Note: Genotypes with high GW **and** low GN (blue color), genotypes with low GW and high GN (red color). Values of YLD, TKW and GN in both treatments are means of three replicates.
ns means not significant effects between treatments.
* Significant different between treatments at P < 0.05.
** Significant different between treatments at P < 0.01.
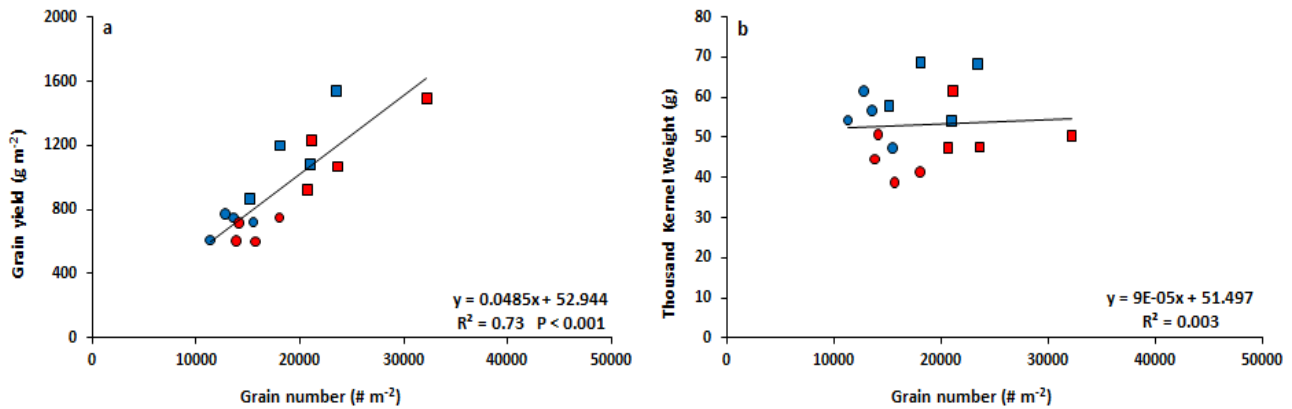*** Significant different between treatments at P < 0.001.

Figure 1. Relationships between grain yield and GN (a) and between average grain weight (TKW) and GN (b) of 8 genotypes evaluated in Valdivia (Chile) during the 2014-2015 growing season. Control treatment (circle symbols) and thinning treatment (square symbols) are shown. Genotypes with high GW and low GN (blue) and genotypes with low GW and high GN (red).
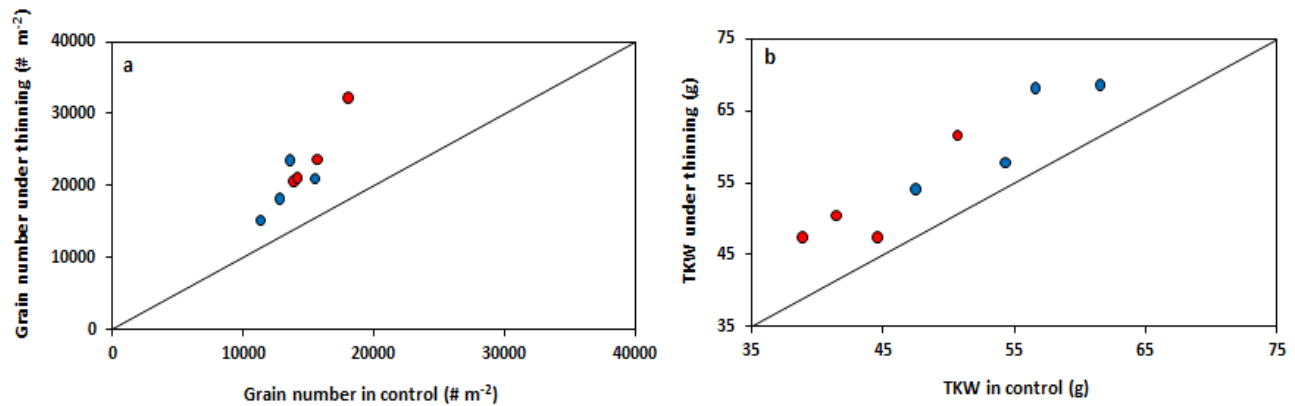

Figure 2. Relationships of grain number (a) and thousand kernel weight (b) between the thinning and control treatments of 8 genotypes contrasting in TKW and GN arrangement evaluated in Valdivia (Chile) during the 2014-2015 growing season. The line shows the 1:1 ratio. Genotypes with high GW and low GN (blue) and genotypes with low GW and high GN (red).

A highly significant association between TKW and grain weight of G2 ($R^2 = 0.89$, $P < 0.001$), and between TKW and grain weight of G4 ($R^2 = 0.45$, $P < 0.01$) was found across genotypes and thinning treatment (Fig. 3). These associations highlight the need of counteracting the trade-off between TKW and GN by increasing the IGW of grains set in both proximal and distal positions of the spike. On the other hand, no association was found between grain weight of both G2 and G4 and GN (Fig. 4), supporting the hypothesis that the trade-off between the two main yield components could be broken.
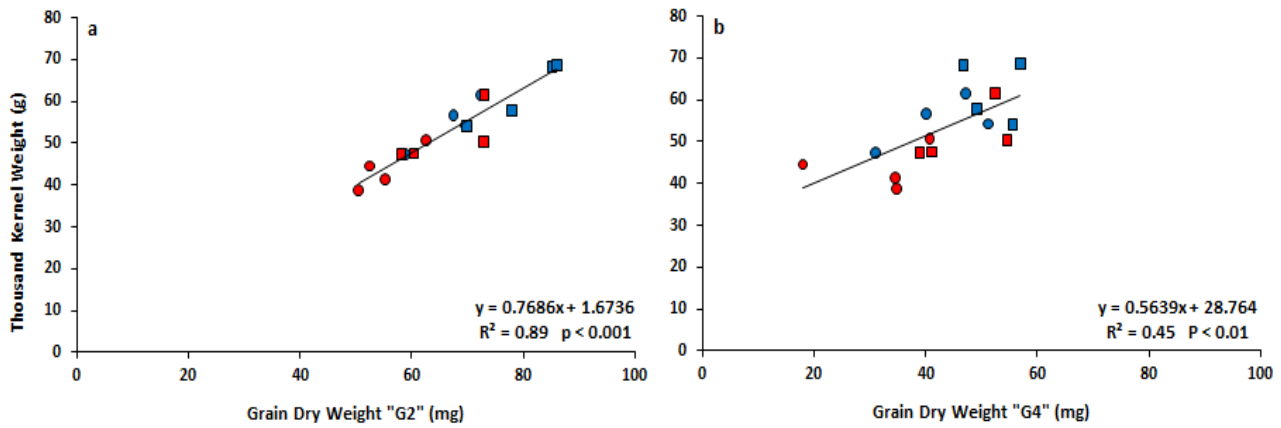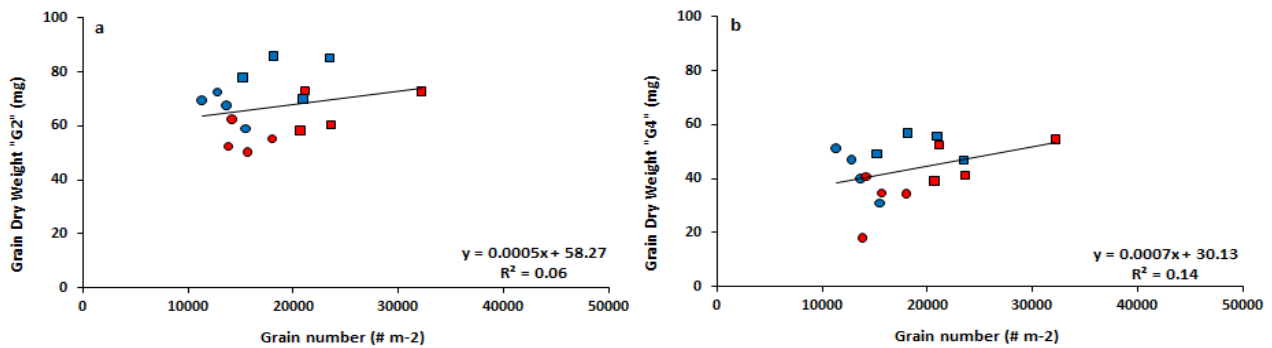
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Figure 3. Relationships between TKW and IKW of G2 (a), and G4 (b) of the 8 genotypes contrasting in TKW and GN arrangement evaluated in Valdivia (Chile) during the 2014-2015 growing season. Control treatment (circle symbols) and thinning treatment (square symbols) are shown. Genotypes with high GW and low GN (blue) and genotypes with low GW and high GN (red).

Figure 4. Relationships of IKW of G2 between GN (a) and G4 (b) and GN of the 8 genotypes contrasting in TKW and GN arrangement evaluated in Valdivia (Chile) during the 2014-2015 growing season. Control treatment (circle symbols) and thinning treatment (square symbols) are shown. Genotypes with high GW and low GN (blue) and genotypes with low GW and high GN (red).

Volume and dimensions (length, width and height) of grain were evaluated in grains G2 and G4 at harvest (Fig. 5 and 6). As expected, the IGW of G2 and G4 had a positive and highly significant relationship with the volume at harvest (Fig. 5a and 6a). Among grain dimensions, the length, width and height of grains were positively associated with the IGW of G2 (Fig. 5b, 5c and 5d) and G4 (Fig. 6b, 6c and 6d). Additionally, IGW of G4 showed good association with both grain length and width (Fig. 6). However, grain length of G2 and G4 seems to be the most promising trait taking into account this trait reached the final value earlier than width and height in the grain filling period (Fig. 7).
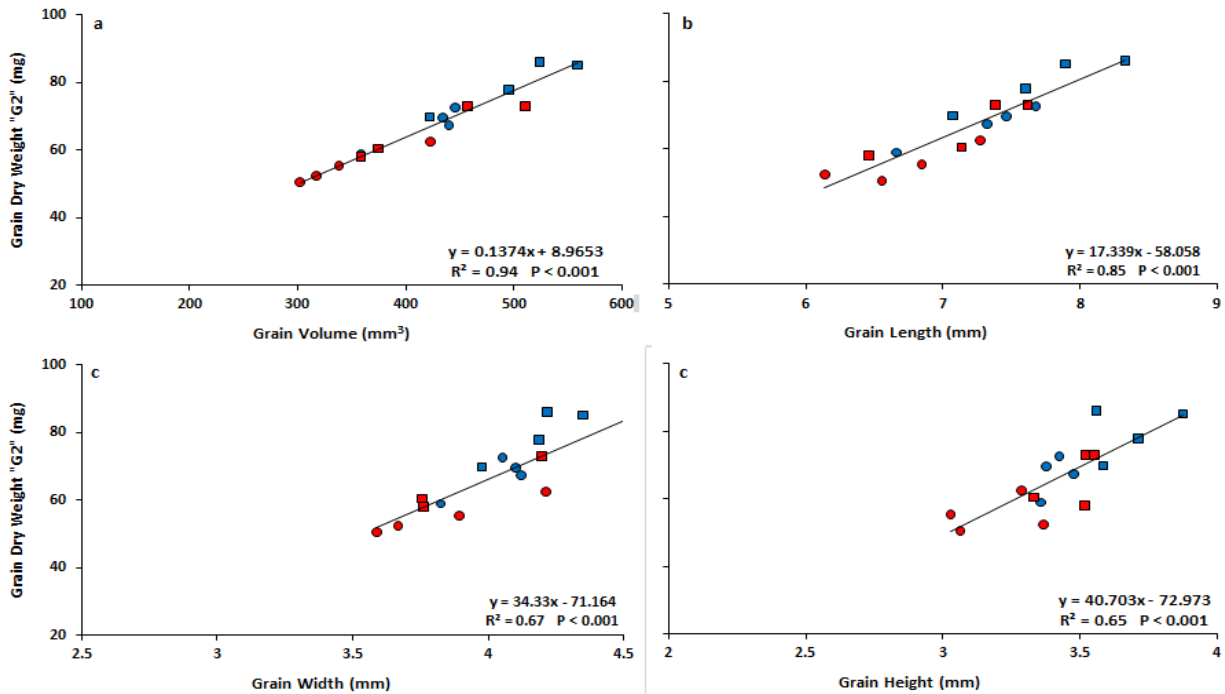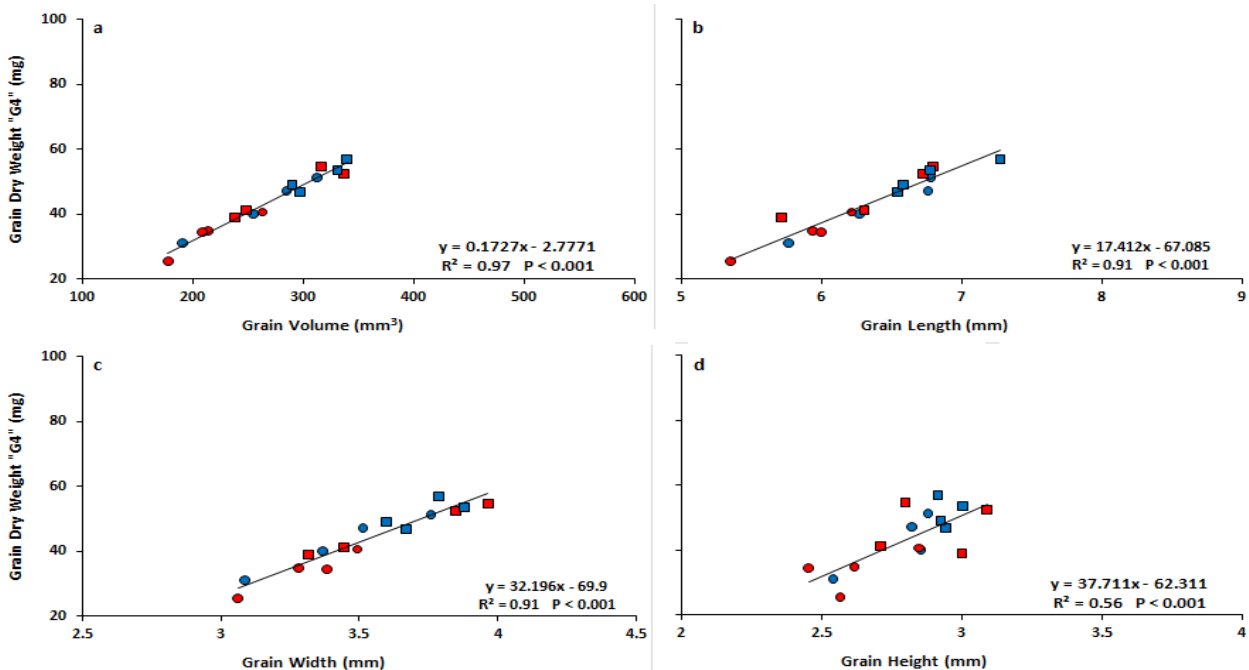
Figure 5. Relationship of IKW of G2 between grain volume (a), as well as the relationships between grain dimensions [grain length (b), grain width (c) and grain height (d)] of the 8 genotypes contrasting in TKW and GN arrangement evaluated in Valdivia (Chile) during the 2014-2015 growing season. Control treatment (circle symbols) and thinning treatment (square symbols) are shown. Genotypes with high GW and low GN (blue), genotypes with low GW and high GN (red).

Figure 6. Relationship of IKW of G4 between grain volume (a), as well as the relationships between grain dimensions [grain length (b), grain width (c) and grain height (d)] of the 8 genotypes contrasting in TKW and GN arrangement evaluated in Valdivia (Chile) during the 2014-2015 growing season. Control treatment (circle symbols) and thinning treatment (square symbols) are shown. Genotypes with high GW and low GN (blue), genotypes with low GW and high GN (red).
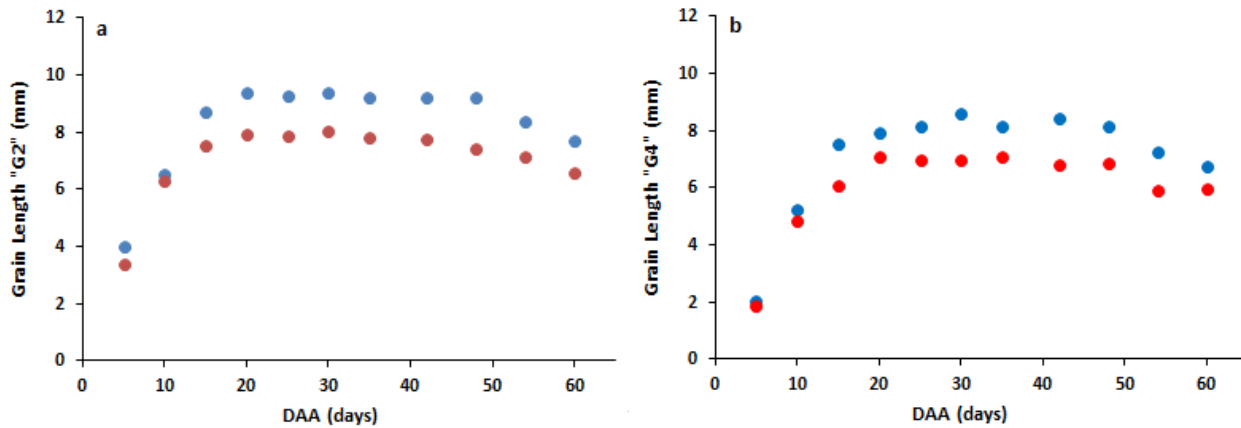
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Figure 7. Relationship of kernel length of G2 (a) and G4 (b) after anthesis in 2 genotypes contrasting in TKW and GN arrangement evaluated in Valdivia (Chile) during the 2014-2015 growing season. Genotype with high GW and low GN (blue) and genotype with low GW and high GN (red).

Conclusions

This study confirms the trade-off between the main yield components reported previously (Bustos et al., 2013; García et al., 2013), including the CIMCOG genotypes (Quintero et al., 2014). However, this trade-off has been lower in Valdivia. The relationship between TKW and IKW of G2 has been confirmed here as well as the predictive value of kernel length about potential kernel weight, showing that this trait and its physiological and molecular drivers are a key for improving TKW. In addition, kernel wide should also be considered, especially in distal kernel positions. Therefore, expansin and GW2 genes controlling are proposed as promising genetic bases of kernel weight of wheat.

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Hormone Concentrations Versus Yield Components: Why is this Information Useful

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Introduction

The complexity of hormone production and its effects on plants raises a lot of questions about their incorporation into plant improvement programmes (e.g. When and what to measure where? At which phenological stage will hormone measurements provide the most explanatory power in both improvement programme and in mechanistic studies?). It is well documented that pre-anthesis is the key phenological stage where grain number per spike and spike per square meter (m^2) can be affected by the environment), while during the post-anthesis stage it is mostly TGW and consequently yield that are impacted. Hormone quantification in key tissues at these key regulatory stages provides us for much scope for analysis

Genotypes do not react similarly to the environment and therefore reduce their yield differently, either by the reduction of grains per spike, or by the number of spikes per m^2, TGW or by combininations of two or three of these responses. In order to determine which hormone(s) is/are relevant to understand some basis of yield resilience, it can important to determine the hormonal signatures in different key tissues at key stages of development. Potentially a very wide range of hormones can be quantified.

One approach to understanding key roles for hormonal regulators is to quantify yield components of different genotypes as affected by mild environmental perturbations. Genetic variation in yield and yield components can then be linked to constitutive variation in hormone signatures and the resilience of these signals under environmental challenge. One hypothesis is that the signalling involved in determination of potential yield takes place via the same set of regulators contributing to a stress response, i.e. in stress biology, we are concerned with a perturbation in a regulatory system rather that at a stress lesion *per se*.

Experimental Material and Stress Treatments

Field experiments were carried out at Cd. Obregon CIMMYT station, Sonora State, NW Mexico (27°20 N, 105°55 W, elevation 39 masl). The experimental material consisted of 10 wheat lines from the CIMCOG(acronym of CIMMYT Core germplasm) panel. These wheat lines were evaluated for one cropping season from February to June 2013 under two-stress environments (heat and drought) and optimal (yield potential) conditions. The drought stress was applied at mid heading stage (65 days after sowing). The sampling consisted in taking, along the phenology, 4 leaves and 4 spikes per plot and freezeing them into liquid nitrogen. This represented 660 samples. The samples were kept in - 80°c and then freeze-dried to be sent to CIMMYT headquarters (El Batan) for grinding before, in turn, being sent to Lancaster University. During this experiment, ethylene gas produced by leaves and spikes was measured once at heading stage under heat conditions in a first selection of 6 genotypes.

In order to associate the susceptibility tendencies determined above to a key phenological stage, seven (7) phenological stages (3 replications) were studied from initiation of booting to anthesis, sampling 4 immature spikes and flag leaves under semi-drought, and 6 phenological (2 replications) stages under heat stress. The samples were taken at 01:00 pm when plants suffer the effects of the highest temperature. Samples were frozen in the field by plunging them into liquid nitrogen. Afterwards, samples were dried using a freeze-dryer and finally ground. The dried ground samples were sent to Lancaster University to be analysed. During this experiment, ethylene gas produced by leaves and spike was measured, at heading stage. A complementary set of hormones has been analysed at this stage (ABA, ACC, CK).

Results

All analysis is carried out within the framework of a newly-developed stress index (Thiry et al. 2015 under internal review). As it has been shown previously, a combination of production capacity and resilience, calculated with yield data under stress and non stress conditions, has demonstrated a high correlation with yield under stress.

In this paper we discuss the relationships between a suite of hormones, the yield, yield components and the stress indices of a range of genotypes. New methods of ethylene sampling are described and differences between ethylene accumulation in different plant parts at different developmental stages are discussed.

Some emphasis is placed on cytokinin accumulation in developing reproductive structures and future plans for perturbation of this key variable are presented.

Conclusions

Analysis of experimental results and relationships between hormones and yield components provide a basis for future plant improvement based on the definition of new physiological traits. Results also provide a clear basis for further experimental work to elucidate the mechanistic basis of yield regulation.

Future Developments:

- Quantitative comparative approaches for genetic potential will be estimated using new stress indices incorporating both estimates of productivity and susceptibility.
- New high throughput hormone quantification techniques will be applied on an organ, plant and plot scale with laser-based technology
- Incorporation of PGR-defined traits (growth, development, yield and physiology) into crop improvement programs.
- PGR-defined progeny will be tested in target environments and promising material specific to stress environments will be identified and assimilated into other pre-breeding activities (targeting International Nurseries and national wheat programmes).
- Mapping population will provide new insight into the physiological and molecular basis of genetic variation in GxExM attributable to PGR effects and will further inform future breeding strategy

Achieving a Step-Change in Harvest Index in High Biomass Wheat Cultivars

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Background

Despite a hypothetical limit to HI of *ca*. 0.65 in wheat (Austin 1982; Foulkes et al. 2011), there has been no systematic progress since the early 1990s from values of ca. 0.45-0.50 in spring wheat and 0.50-0.55 in winter wheat (Foulkes et al. 2011; Reynolds et al. 2012). Evidence shows that the latest progress in yield potential of CIMMYT spring wheat in the Yaqui Valley from 1990 to 2009 in semi-dwarf cultivars is associated with greater above-ground dry matter and grain weight, but decreases in HI over the same period (Aisawi et al. 2015). In this scenario, it seems that biomass is an important determinant of genetic gains in yield potential but it will be crucial to identify traits and markers enabling breeders to discriminate "useful" and "non useful" biomass to maximize partitioning to the grains, not only for current new high biomass cultivars but also at even higher levels of biomass anticipated from impacts in the area of photosynthesis research.

While allocation of carbon to the developing wheat spike determines grain sink strength (a major determinant of yield potential), concurrent growth of other organs competes for carbon (Fischer 1985; Foulkes *et al*. 2011; Reynolds *et al*. 2012). Partitioning to spikes could be increased by reducing competition from alternative sinks, especially during stem elongation when grain number is determined. These competing sinks include roots, leaves, stems (structural and soluble carbohydrate DM), and infertile tillers. A potential avenue to increase spike partitioning and HI is to decrease true-stem DM partitioning while increasing the material strength of the stem to maintain lodging resistance (Foulkes et al. 2011). True-stem DM is partitioned between structural and redistributable components, and increasing the proportion of soluble DM has been shown to favor HI in irrigated spring wheat cultivars in northwestern Mexico (Saint Pierre et al. 2010). Strategies to boost spike growth by reducing assimilate partitioning to alternative sinks are complementary to those to optimizing phenology. Optimizing partitioning to favor the spike will mainly increase the rate of spike growth, whereas optimizing phenology will mainly extend the duration of spike growth in the pre-anthesis phase.

The complementary trait to spike partitioning, that may be improved to further enhance grain number, is the fruiting efficiency (ratio grain number to spike DM at anthesis, FE) (Foulkes et al. 2011; Lázaro and Abatte 2011). There is clear variability among modern cultivars in FE (González *et al*. 2011; Lázaro and Abatte 2011). Although a trade-off between these two physiological components is often observed (Gonzalez *et al*. 2011), encouragingly recent work has demonstrated the possibility to identify genotypes combining high spike DM with a high FE (Lázaro and Abbate 2011).

We aimed to: (i) identify genetic sources of wheat expressing favorable values of assimilate-partitioning traits and fruiting efficiency to achieve a step change in HI through screening genetically diverse germplasm and (ii) identify novel traits and mechanisms determining genetic variation in spike partitioning, fruiting efficiency and HI.

Summary of Results

Analysis of DM partitioning and spike fertility traits in 26 genotypes of the CIMCOG (CIMMYT Mexico Core Germplasm) I panel was carried out in 2011-2012 and 2012-2013 at the Norman E. Borlaug Field Experimental station, Ciudad Obregon. Experiments were grown on raised beds under fully irrigated conditions in a lattice design with three replicates. The CIMCOG panel is comprised mainly of high yield potential CIMMYT cultivars and advanced lines including high biomass selections and also includes several historic cultivars.

Relationships between yield potential and physiological yield components

Grain yields of the best yielding cultivars were c. 7.5 t ha^{-1}, compared to less than 6.0 t ha^{-1} for the worst. Anthesis date (GS65) of the 26 genotypes ranged from 78-97 days after sowing. HI was positively associated with grain yield amongst genotypes ($R^2 = 0.30$; $P< 0.001$; Figure 1a). The relationship was non-linear (quadratic) so that yield increased with HI up to ca. 0.49 and then levelled off. Overall HI ranged amongst the 26 genotypes from 0.45-0.51 ($P< 0.001$). These values are much less than the theoretical maximum of ca. 0.65 (Austin 1982; Foulkes et al. 2011) indicating significant scope for raising yield through improved HI in modern CIMMYT cultivars. A negative linear relationship between HI and above-ground biomass ($R^2 = 0.17$; $P< 0.05$; Fig. 1c) indicated that the highest biomass cultivars were less efficient at partitioning assimilate to grain; therefore, novel traits to maximize partitioning to "useful" biomass must be identified.
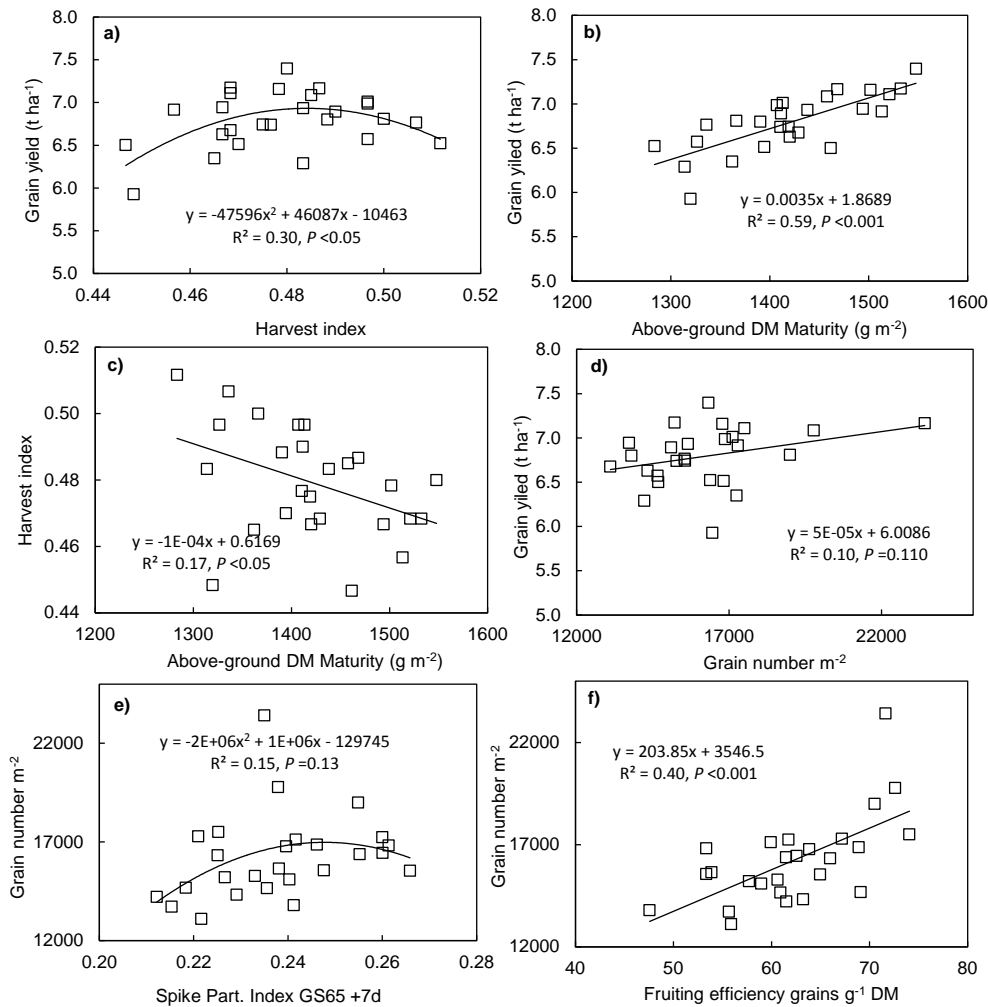
Figure 1. Regressions of a) grain yield on HI, b) grain yield on above-ground DM, c) HI on above-ground DM, d) grain yield on grains m^{-2}, e) grains m^{-2} on spike partitioning index and f) fruiting efficiency on grains m^{-2} for 26 CIMMYT spring wheat cultivars. Values represent means 2011-2012 and 2012-2013.

Results showed a weak positive non-linear (quadratic) association between spike partitioning index (proportion of above-ground biomass in spike, SPI) and grains m^{-2} at GS65+7d amongst the 26 CIMCOG genotypes ($R^2 = 0.16$, $P= 0.13$; Figure 1e). There was a stronger positive linear association between the fruiting efficiency at GS65+7d and grains m^{-2} ($R^2 = 0.40$, $P<0.001$). Plant height ranged from 84-116 cm ($P< 0.001$), and showed a trend for a negative association with HI ($R^2 = 0.12$, P = 0.09; data not shown), but was not overall associated with grain yield or above-ground biomass.

Relationship between HI and plant component partitioning at anthesis
Spike partitioning index ranged amongst cultivars from 0.21-0.27 ($P< 0.001$) and was positively linearly associated with HI ($R^2 = 0.16$, $P< 0.05$; Fig. 2a). The proportion of the true-stem DM present as water soluble carbohydrate (WSC) at GS65+7 d ranged from 0.11-0.38 ($P< 0.001$) and was also positively linearly associated with HI ($R^2 = 0.11$, P = 0.09; Fig. 2b).

Spike partitioning index was linearly negatively associated amongst genotypes with true-stem PI at GS65+7d ($R^2 = 0.35$, $P< 0.01$; Figure 3); there was no association of SPI with leaf-sheath PI or leaf-lamina PI (Figure 3). Overall these results indicated that, in modern high yield potential CIMMYT cultivars, the true-stem component is competing most strongly with spike growth. In order to reduce true-stem partitioning in the most effective way, it will be necessary to identify those true-stem internodes which are competing most strongly with stem growth during stem elongation.
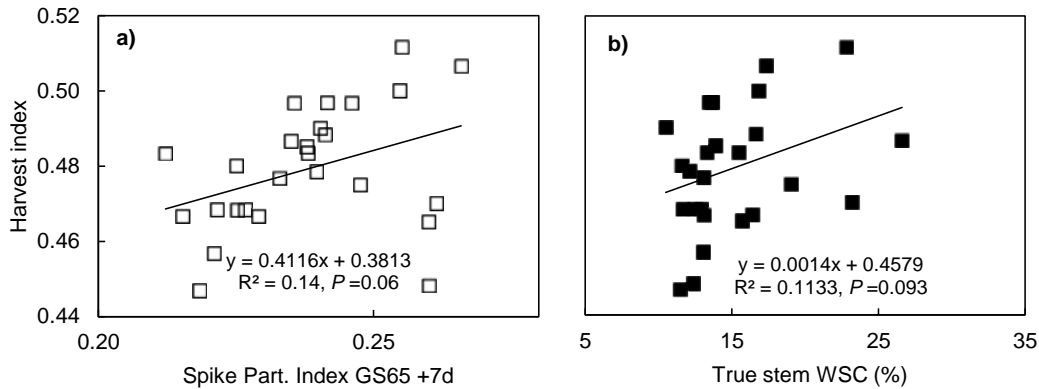
Figure 2. Linear regressions of a) HI on spike partitioning index and b) HI on true-stem water soluble carbohydrate percentage at GS65+7d. Mean values in 2011-2012 and 2012-2013.
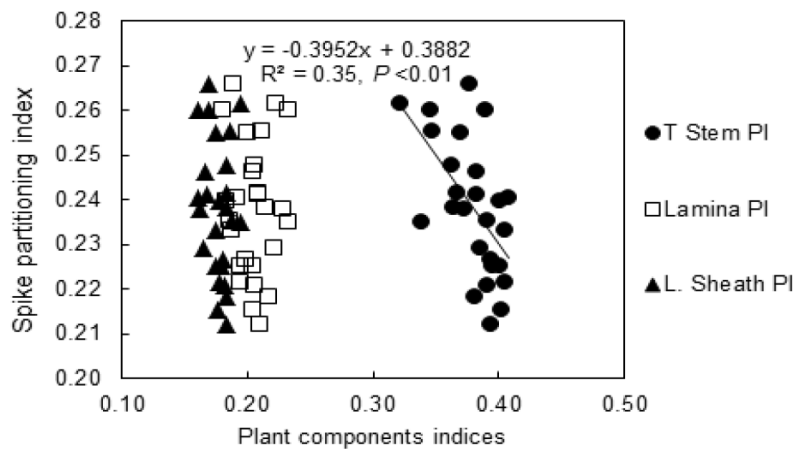

Figure 3. Relationships between spike, true stem, lamina and leaf sheath DM partitioning indices (proportion of total AGDM) at GS65+7d for 26 CIMCOG genotypes. Mean values in 2011-2012 and 2012-2013.

Relationship between spike partitioning index and internode partitioning

We investigated the association of DM partitioning to true-stem internodes (peduncle, internode 2, 3, and 4+) with SPI amongst a subset of 9 CIMCOG genotypes with a restricted range in anthesis date (Figure 4). Negative associations between SPI and internode 2 partitioning index (PI) and internode 3 PI were found ($P<0.05$; Figure 4); no associations were found for peduncle PI or internode 4+ PI. This indicates growth of the 2nd and 3rd internodes competes most strongly with spike growth. Assuming 5 extended internodes per shoot, extension of the 3rd internode typically occurs before booting, and of the 2nd internode typically occurs during booting and spike emergence. The lack of a correlation between SPI and peduncle PI may reflect a significant proportion of peduncle extension occurs after anthesis.
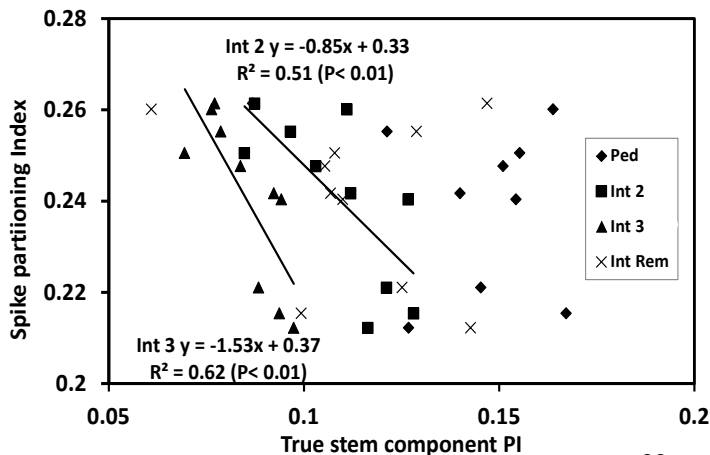

Figure 4. Linear regression of spike partitioning index and DM partitioning amongst true-stem internodes (peduncle (Ped), internode 2 (Int 2), internode 3 (Int 3) and internode 4+ (Int Rem) at GS65+7d for 9 CIMCOG genotypes Mean values in 2011-12 and 2012-13.

33

Optimized distribution of structural and soluble carbohydrate amongst plant organs

The average allocation of dry matter to plant components at GS61+7d as either fixed structural DM or soluble redistributable DM is shown in Figure 5 together with the genetic ranges. The design targets to maximize partitioning to "useful biomass" in high biomass cultivars include: i) reduced DM partitioning to true stem and ii) increased DM partitioning to true- stem soluble carbohydrate. Our results demonstrate that spike partitioning index can be increased from the current maximum value in the CIMCOG panel of 0.32 to 0.38 by exploiting existing variation for partitioning within the CIMCOG panel, i.e. by combining minimum expression of partitioning indices for competing plant components (leaf lamina, leaf sheath, true stem) observed in the panel (Figure 3).
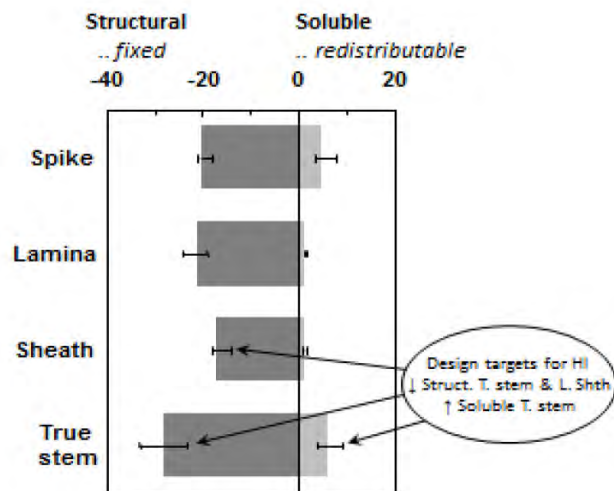

Figure 5. Available genetic variation in DM partitioning (percentage of above ground DM 7 days after anthesis (%)). Bars represent genetic range (LHS axis) and soluble (RHS axis)at anthesis (GS65+7d).

Relationship between within spike partitioning and the fruiting efficiency

Averaged across 2012 and 2013, genetic variation in grains m^{-2} was mainly explained by FE rather than SPI. For a subset of 7 genotypes, with a restricted range in anthesis date representative of the full range in FE in the 26 genotypes, a detailed analysis of spike partitioning at harvest (rachis, glume, palea, lemma, awn) was carried out. Results indicated a positive linear association between the partitioning of spike DM to the lemma and the FE (r = 0.84, *P*< 0.01; Fig. 6a).

It can be speculated that a larger lemma fraction may favor floret survival through enhanced lemma photosynthesis and/or that larger lemmas may be associated with a relatively greater assimilate supply within the spike to developing florets which are initiated in the axils of the lemmas. In addition, decreased rachis specific weight was associated with higher FE (Fig. 6b).
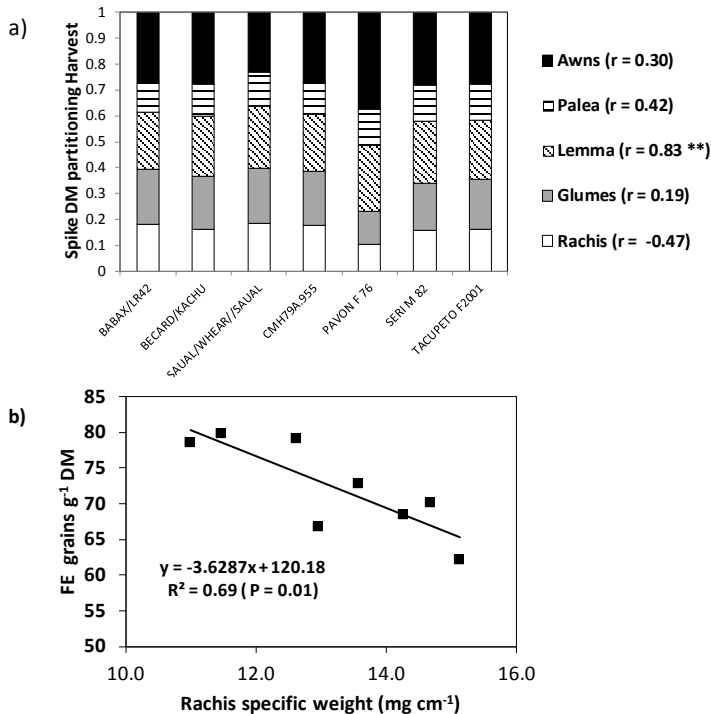

Figure 6. a) Partitioning of spike (chaff) DM at harvest and correlations with the fruiting efficiency (FE) for 7 CIMCOG genotypes (mean 2011-2012 and 2012-2013) and b) rachis specific weigh versus fruiting efficiency for 9 CIMCOG genotypes in 2011-2012).

34

Implications for Yield Potential

Our results show strong evidence that grain partitioning is not optimized to take advantage of high biomass and moreover there is unutilized genetic potential that can be exploited. Our analysis in the CIMCOG panel in 2011-2012 - 2012-2013 has shown that increased harvest index is most likely to be achieved from combinations of novel traits that include: (1) decreased true-stem DM partitioning to internodes 2 and 3, (2) enhanced partitioning to the soluble DM component of during stem elongation and (3) enhanced fruiting efficiency, associated with decreased rachis specific weight and increased lemma fraction. Our data has shown that there is sufficient variation within the CIMCOG panel for these novel traits to achieve a step change in HI in CIMMYT spring wheat to 0.60 from the current maximum value of 0.51 by combining within a novel plant ideotype the biggest expression for 'useful' biomass traits for grain partitioning, including: decreased partitioning to internodes 2 and 3 (0.206; Babax/LR42) to enhance spike growth and decreased rachis specific weight (11.0 mg cm^{-1}; Becard/Kachu) and increased lemma fraction (0.256; Pavon) to enhance fruiting efficiency (Figures 3 and 6). We have identified subsets of germplasm with highest expression of these favorable traits (whilst minimizing trade-offs) for strategic crosses in pre breeding at IWYP-PLAT. Applying the knowledge and phenotyping techniques developed here in genetically characterized panels will allow us to maximize exploitation of the radiation-use efficiency advances of IWYP by developing novel traits and molecular markers for "useful biomass".

Acknowledgments

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Structural Requirements of Irrigated Spring Wheat to Avoid Lodging

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Background

Lodging is defined as the permanent displacement of plant stems from their vertical position as a result of wind acting on the stem, and rain or irrigation weakening the soil leading to reduced stem and anchorage strength (Berry et al. 2004). This phenomenon reduces wheat productivity by adversely affecting grain quality (Berry et al. 2004) and reducing grain yield by up to 80% (Easson et al. 1993; Berry and Spink 2012). Reduced height with the introduction of dwarfing genes to wheat during the Green Revolution has increased lodging resistance, however, further reduction of plant height may be limited because these genes could have a direct negative effect on the final grain weight (Miralles and Slafer 1995), reduce water soluble carbohydrate storage capacity (Cossani and Reynolds 2012) and reduce leaf extension rate (Keyes et al. 1989). A minimum plant height compatible with high yields was estimated at between 0.7 to 1.0 m (Flintham et al. 1997) and has been reached in many environments. Wheat height has remained static for several years in some countries such as the UK (Berry et al., 2014). Recently, Quantitative Trait Locus (QTL), which increase height and yield have been identified (Berry and Berry 2015). This discovery may help to explain why plant breeders have found it difficult to improve yield and reduce height simultaneously.

A mechanistic validated model of lodging in wheat (Baker et al. 1998; Berry et al. 2003*b*) calculates the wind speed required to cause lodging based on crop characteristics (e.g. height, yield, stem strength, anchorage strength). The lodging model has identified genetic variation for the stem and anchorage strength of winter wheat in the UK (Berry et al. 2003*a*, 2007). The identification of traits involved in the strength of the stem and root anchorage (stem diameter, wall width, material strength and root plate spread, structural rooting depth) represents a new alternative for breeding for lodging resistance. However, more understanding of the genetic control of these traits and possible trade-offs with yield will be required.

A preliminary attempt to quantify the stem strength and anchorage strength required by winter wheat to withstand a 1 in 25 year wind gust in the UK by using the lodging model has been made by Berry et al. (2007). This indicated that substantial amounts of dry matter must be invested in the stem and anchorage system to make plants lodging-proof. This would mean that the maximum harvest index (ratio of grain dry matter to above-ground dry matter) for a 0.7m tall crop yielding 8 t ha^{-1} would only be 0.42, rising to 0.50 for a crop yielding 16 t ha^{-1}, which is significantly less than the theoretical maximum harvest index of 0.62 estimated by Austin et al. (1980). Additionally, it is possible that the investment in dry matter for the stem and anchorage system may compete for resources with grain yield determination. The aim of this paper is to quantify the dimensions of spring wheat plants required to avoid lodging in northwest Mexico (NWM) and considers the dry matter that must be invested in support structures to achieve this.

Data Source

Lodging-related traits, water soluble carbohydrate content (WSC) and stem and root biomass were measured on 60 elite spring wheat lines conforming the CIMMYT Mexico Core Germplasm Panel (CIMCOG) (including 58 *T. aestivum* and two *T. durum* lines) during 2011 and 27 lines (including 26 *T. aestivum* and one *T. durum* lines) during 2012 and 2013 and 5 lines during 2014 at CENEB (Centro Experimental Norman E. Borlaug) in the Valle del Yaqui, Sonora, Mexico (27.9°N and longitude 109.9°W). Trials were established using an alpha lattice design under the raised bed sowing system and local conventional agricultural management was used to grow the crop under optimal conditions for yield potential. Characterization of the wind for the NWM region used local met station data from 40 years and used the method described by Piñera-Chavez et al., (2014). It was estimated that the period when the crop was at risk to stem lodging was 50 days and the period when the crop was at risk to root lodging was 10 days (when the soil was wet and weak enough following irrigation to permit anchorage failure).

Summary of Results

Wind gust speed probabilities

The probabilities for experiencing gust speeds at the height of the crop during the stem and root lodging risk periods at NWM are summarized in Figure 1. The wind gusts with a 25 year return period were calculated as 22 ms^{-1} for stem lodging and 18 ms^{-1} for root lodging. The wind gusts with a five year return period were calculated as 18 ms^{-1} for stem lodging and 14 ms^{-1} for root lodging.
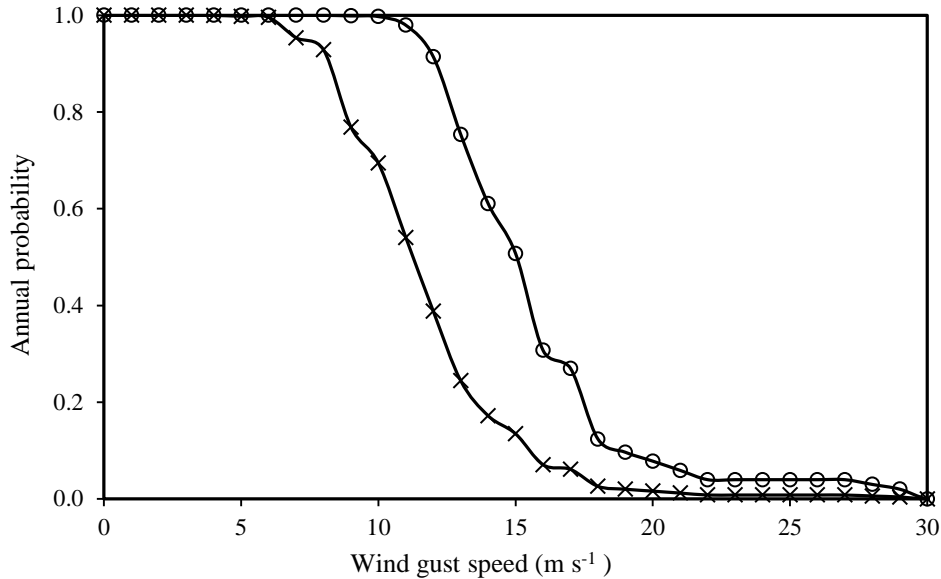
Figure 1. NW Mexico seasonal maximum wind gust probabilities for 50 days of high stem lodging risk (○) and for 10 days of high root lodging risk (when surface soil horizon is moist) (×)

Biomass and failure moment of stem and anchorage system

A positive regression (R^2 = 0.63; P < 0.001) between the structural stem dry matter per unit length and internode failure moment for internodes 1 to 2 (27 genotypes, 2011, 2012, 2013 and 2014) and internodes 3 to 4 (5 genotypes, 2013 and 2014) showed that both traits were strongly correlated in spring wheat. According to this regression model where the response variable was the internode failure moment, a fitted value of 100 N mm in this parameter could be achieved with a structural stem dry weight per unit length of 1.13 mg mm^{-1} or with 1.53 mg mm^{-1} of overall stem dry weight including WSC (Fig. 2). There was no association between WSC content and internode failure moment for any internodes. There was a positive association between root dry weight per plant and root plate spread among 27 genotypes which had a consistent slope across years 2012 and 2013 but different intercept with an R^2 of 0.74 (P < 0.001).
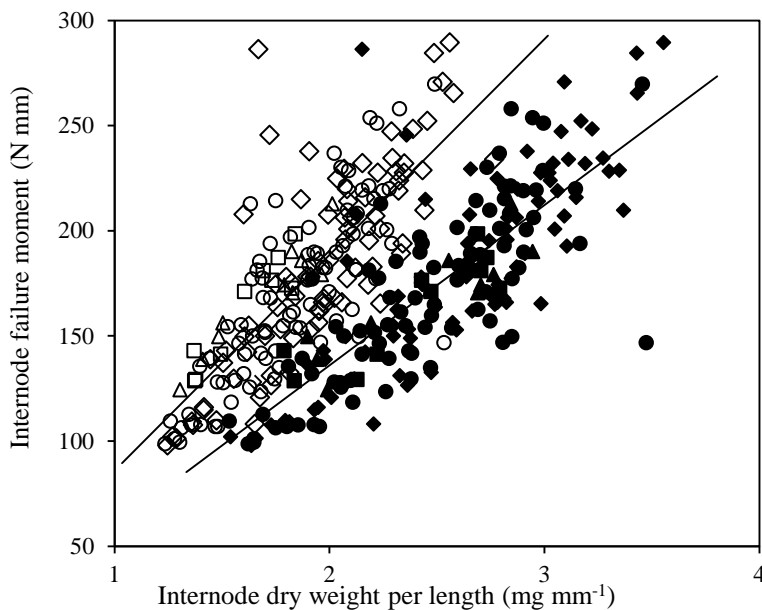

Figure 2. Dry weight per unit length against failure moment of internode 1(diamonds), internode 2 (circles) for 27 genotypes (2011, 2012 and 2013 experiments) and of internodes 1, internode 2, internode 3 (triangles) and internode 4 (squares) for five genotypes (2013 and 2014 experiments). Open symbols indicate structural dry weight (y = 103x – 16.8; R^2 = 0.63) and closed symbols indicate overall dry weight (y = 76.2x – 16.3; R^2 = 0.64)

Calculating the lodging-proof ideotype

The predicted size of the root plate, stem diameter and stem failure moment required to avoid lodging for a range of crop types and lodging return periods have been estimated by the lodging model and are described in Table 1.

Table 1. NWM ideotype trait targets for different lodging return periods

Character	Lodging return period (years)			
	5	10	15	25
0.7 m tall and 6 t ha⁻¹				
Root plate spread (mm)	43.2	47.3	49.2	51.1
Stem diameter (mm)	3.51	3.67	3.97	4.12
Stem failure moment (N mm) (stem strength)	179	200	244	268
0.7 m tall and 10 t ha⁻¹				
Root plate spread (mm)	46.1	50.4	52.5	54.5
Stem diameter (mm)	3.79	3.96	4.29	4.45
Stem failure moment (N mm) (stem strength)	218	243	296	325
1.0 m tall and 6 t ha⁻¹				
Root plate spread (mm)	49.1	53.7	55.9	58.1
Stem diameter (mm)	4.09	4.27	4.63	4.82
Stem failure moment (N mm) (stem strength)	263	293	358	393
1.0 m tall and 10 t ha⁻¹				
Root plate spread (mm)	52.5	57.4	59.8	62.1
Stem diameter (mm)	4.43	4.63	5.03	5.24
Stem failure moment (N mm) (stem strength)	321	358	437	480

* Stem traits are for the bottom internode and which is assumed to have a stem wall width of 0.65 mm and Material strength of 50 Mpa

Quantifying stem and root biomass requirements of a lodging-proof wheat crop

The amount of stem and surface root dry matter for a range of crop types and lodging return periods (Figure 3) were estimated from the relationships between stem strength (stem failure moment) and root plate spread with biomass that were described earlier. This shows that a substantial amount of stem biomass must be invested in the support structures of the plant for it to withstand a wind gust with a return period of 25 years.
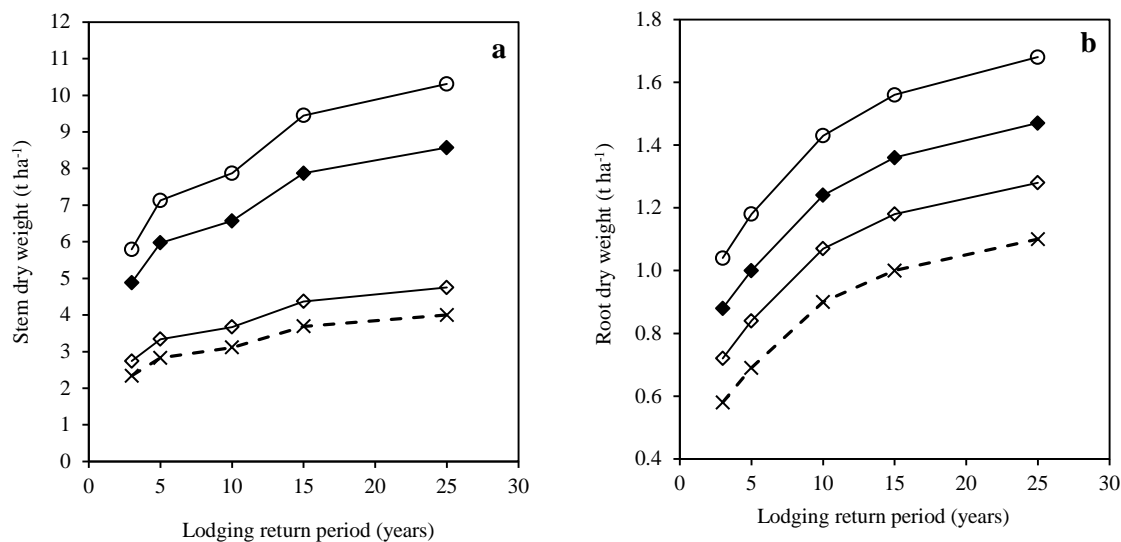

Figure 3. Stem (a) and root dry weight (b) for a crop yielding 6 t ha⁻¹ with a crop height of 1.0 m (♦) and 0.7 m (×), and crop yielding 10 t ha⁻¹ with a crop height of 1.0 m (○) and 0.7 m (◊), for different lodging return periods in the NWM environment. Dotted line indicates crop with current average yield of 6 t ha⁻¹ and putative minimum crop height compatible with this yield of 0.7 m

Discussion

The strong positive relationships between the stem structural biomass per unit length and stem strength (stem failure moment), and root plate spread with root surface biomass demonstrate that breeding for greater yield and lodging resistance will be challenging unless total biomass can be increased. Even with greater biomass, careful optimization of yield and lodging traits will be required to minimize the inevitable trade-offs between traits that develop at the same time. For example, it is understood that the most useful investment of stem biomass for stem strength is in the production of wider stems and stronger material strength, rather than thicker stem walls. It is possible that a shorter lodging return period will have to be accepted in order to maximize average grain yield over several years. A combination of genetic dissection of biomass and lodging traits, together with modeling to identify optimum combinations of traits and genetic markers, will be required to increase yield and lodging resistance.

Acknowledgments

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Towards the Manipulation of Floral Development to Increase Grain Yield in Wheat — A physiological and Genetic Approach

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Background

Genetic gains in wheat yield are to a greater degree related to grain number, rather than to the average grain weight (Fischer 2008 2011), as yield is mostly sink-limited during grain-filling (Serrago et al. 2013). Consequently large gains in yield can be only expected through gains in grain number (Slafer et al. 2014), the most plastic of the yield components (Sadras and Slafer 2012). Grain number is largely determined during the stem elongation (SE) period (Fischer 1985; Slafer and Rawson 1994). Before becoming grains, floret primordia start developing sometime around the initiation of terminal spikelet, which typically coincides with the beginning of SE, and the final number of fertile florets is set at anthesis. It is likely that the duration of the stem elongation phase, within adaptive constraints, is a major determinant of floret number (Miralles et al. 2000; Whitechurch et al. 2007). In aspiring to manipulate grain number and therefore yield, one approach is to manipulate the length of SE. However, to ensure that as many florets as possible are converted to grain it is important to understand the dynamics of floret production. Within the indeterminate spikelets of wheat many more florets are initiated than grains finally produced. This is largely due to floret abortion (Gonzalez et al. 2011).

In this study, we have investigated both processes: the implications of different floret development/abortion profiles in selected lines of the CIMMYT Mexico Core Germplasm (CIMCOG) population; and the genetic control of the duration of SE through Quantitative Trait Locus (QTL) analysis in the Buster x Charger doubled haploid population. The long term breeding goal is to provide the tools and knowledge to achieve an increase in the period where resources are being partially allocated to the generation of florets, allowing for labile primordia to further develop reducing the risk of mortality (Gonzalez-Navarro et al. 2015) and find genes and alleles that can be selected to extend the period of SE. Finally, we are producing a new set of genetic resources that will enable us to extend this type of analysis to wider CIMMYT germplasm making sure that all of the carbon captured in new high biomass materials is channeled into grain yield.

Summary of Results

The variation in number of fertile florets within a representative subset of the CIMCOG elite germplasm was much better related to the survival of floret primordia than to the maximum number of florets initiated; both components had a significant variation (Figure 1). This shows that selection for floret survival, rather than peak floret number is likely to be the most productive strategy to increase grain number.
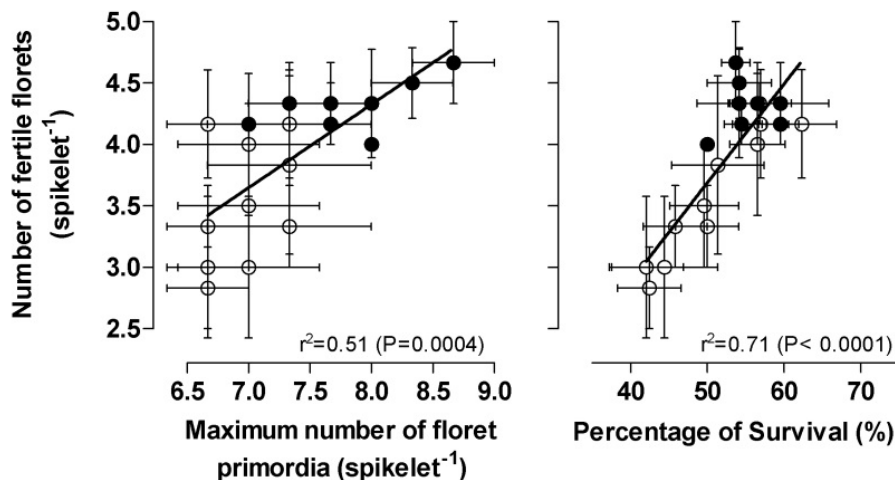

Figure 1. Number of fertile florets per spikelet related to either maximum number of floret primordia initiated (left panel) or the percentage of these primordia which developed normally in to fertile florets (right panel). Open circles represent season 2010-2011 and close circles season 2011-2012.

An in-depth analysis of line 8 and 9, highest and lowest spike fertility respectively, showed that the two floret primordia proximal to the rachis were mostly fertile, while the most distal florets (florets 6–8) never reached a fertile stage, pinpointing the difference in number of fertile florets to the developmental patterns of intermediate florets (floret primordia 3, 4 and 5). It seems that florets started its development in line 9 with some delay compared to timing of development initiation on line 9 (Figure 2). Genotypes with a higher number of fertile florets exhibited an improved survival of floret primordia that relates to a longer period of development.
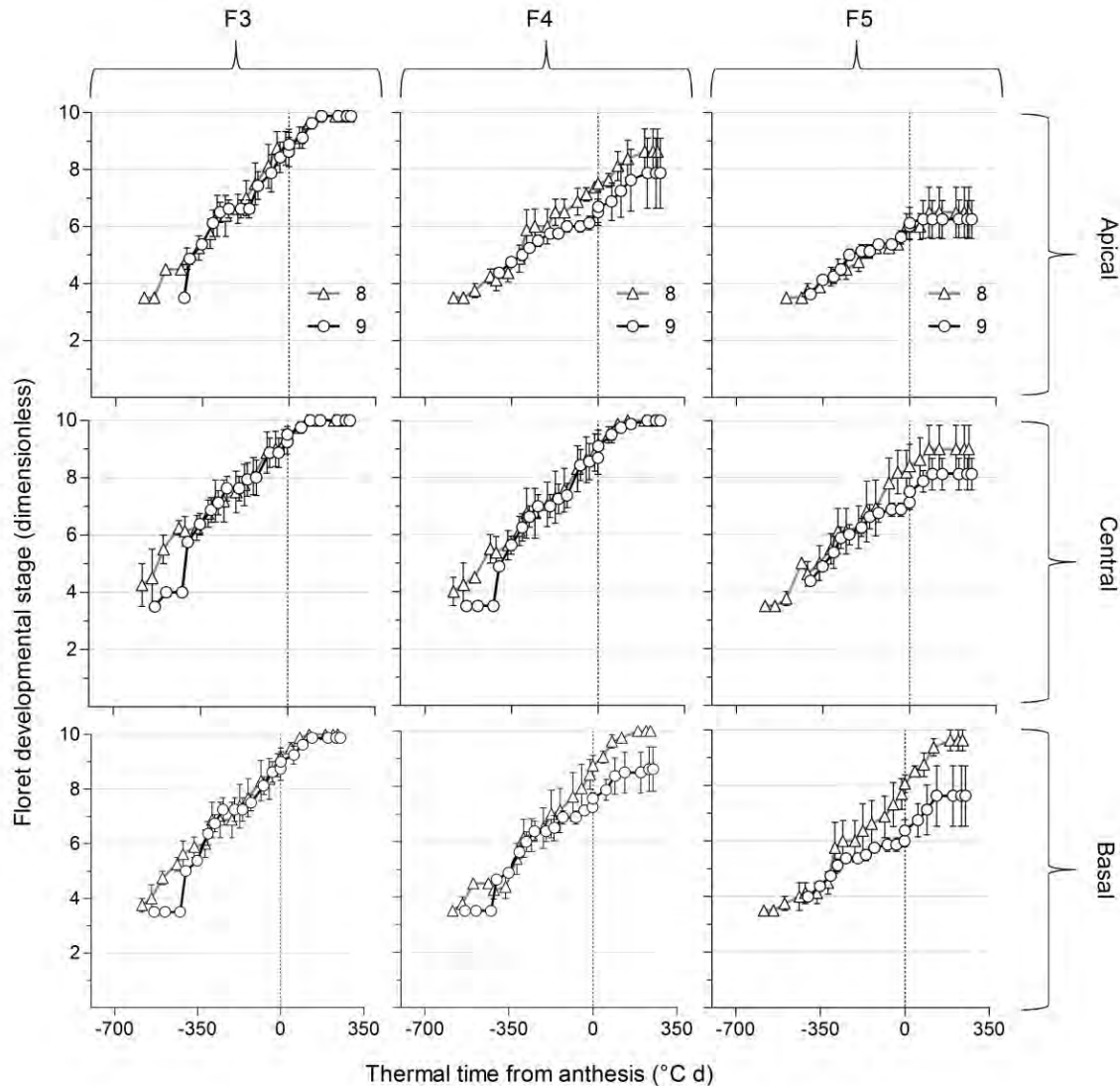

Figure 2. Developmental progress of floret primordia 3, 4 and 5 (from left to right panels) in apical, central and basal spikelets (from top to bottom panels) from the onset of stem elongation onwards, plotted against thermal time from anthesis in genotypes 8 and 9.

In order to locate chromosomal positions affecting the time to the beginning and end of SE, three seasons of field experiments with a doubled haploid population of Buster x Charger were carried out using a 90K Illumina SNP based map developed within the EU FP7 project ADAPTAWHEAT. This analysis confirmed the presence of a QTL in chromosome 7A for time to terminal spikelet and two QTLs in chromosomes 2D and 4A with an effect on time to heading (Figure 3). Independent genetic control of time to TS and heading show that marker assisted selection could be deployed to manipulate SE duration.
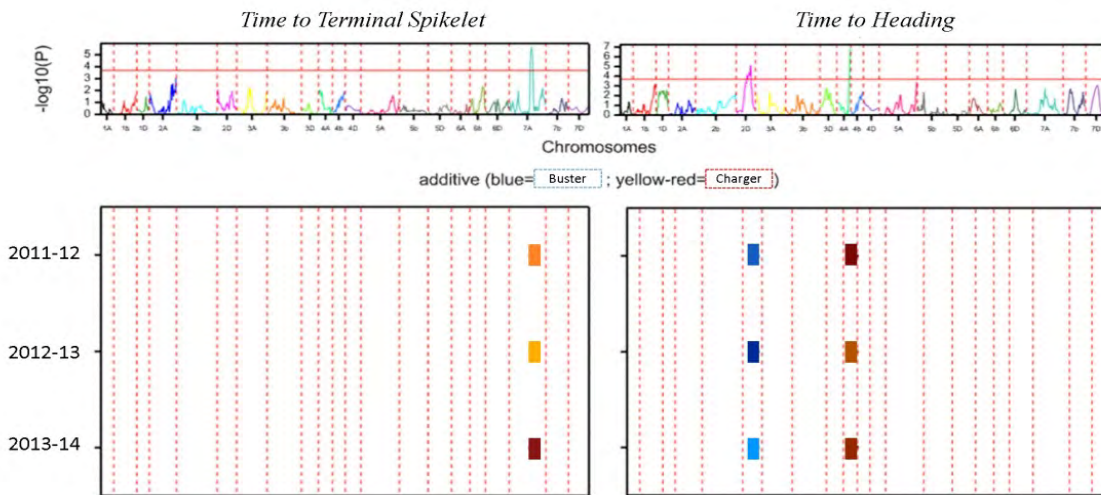
Figure 3. Multi-environment QTL analysis for SE landmarks.

Implications for Yield Potential

Alternative ways to further increase yield by breeding are urgently required to maintain current levels of food security. Among other traits, further increases in yield potential are dependent on adaptation and fine-tuning of wheat development (Reynolds et al. 2012). Being able to allocate each major developmental stage to the optimal weather condition, seem like a must within the context of climate change. In the work developed so far (whose results are outlined above) we proved the relevance of floret development as a major determinant of grain number (and yield) in wheat and identified QTLs in a mapping population related to the partitioning of developmental time to heading which might be a driving force for differences in floret development. However, to translate this into trustworthy tools for realistic breeding programs we must reconfirm the value of the traits (developmental partitioning and floret survival associated to it) in strategic crosses designed to produce breeding populations for improved yield potential and identify molecular markers in these realistic populations. Therefore, in order to extend the approach outlined above and our other studies of CIMMYT germplasm (Griffiths et al. 2015) we have developed segregating populations using CIMCOG varieties as founders and two common parents, Paragon (UK spring wheat) and Weebill (CIMMYT spring wheat). These populations will allow us to describe the genetic architecture of SE and floret dynamics so that these difficult to score traits can be manipulated by marker assisted selection.

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Dissection of Yield Potential Related Traits: What Shall We Focus On?

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Background

Conceptual models of desirable trait profiles are used in wheat breeding to accumulate complementary physiological traits (Reynolds *et al.*, 2009*b*). Whereas physiological breeding efforts have been focused on improving crop adaptation to abiotic stresses (Reynolds *et al.*, 1998; Condon *et al.*, 2004; Reynolds *et al.*, 2005; Richards, 2006; Reynolds *et al.*, 2009*b*), interest in raising the yield potential has grown recently (Reynolds *et al.*, 2009*a*, 2011) with promising results to date (Reynolds *et al.* 2014; Reynolds *et al.*, *2015*). Under yield potential conditions, the conceptual models of traits encompass a large diversity of the potential mechanisms that are based on a combination of empiricism within a limited range of environments, as well as some speculation based on the theory (Reynolds *et al.*, 2009*b*). The identification of these traits and the importance of them should be assessed by whether they fit into frameworks that are appropriate to improve yield. In this sense, only those traits of economic importance showing genetic variation and high heritability can be considered for improvement in the context of plant breeding (Jackson, 2001).

It is generally assumed that the genetic diversity for certain traits in elite material is scarce (Able et al., 2007). However, few studies have determined genotypic variation for yield potential related traits in elite wheat lines. Therefore, we can consider these assumptions more theoretical than derived from empirical evidences. The main traits presented in Figure 1 where studied for three years at MEXPLAT (NW-Mexico) in the CIMCOG panel (CIMMYT Core Germplasm) composed by elite wheat lines including the most advanced lines provided by CIMMYT breeders and some historical lines. This work is part of a series of studies related with Wheat Yield Consortium (WYC) activities aiming to achieve yield potential (Figure 1).

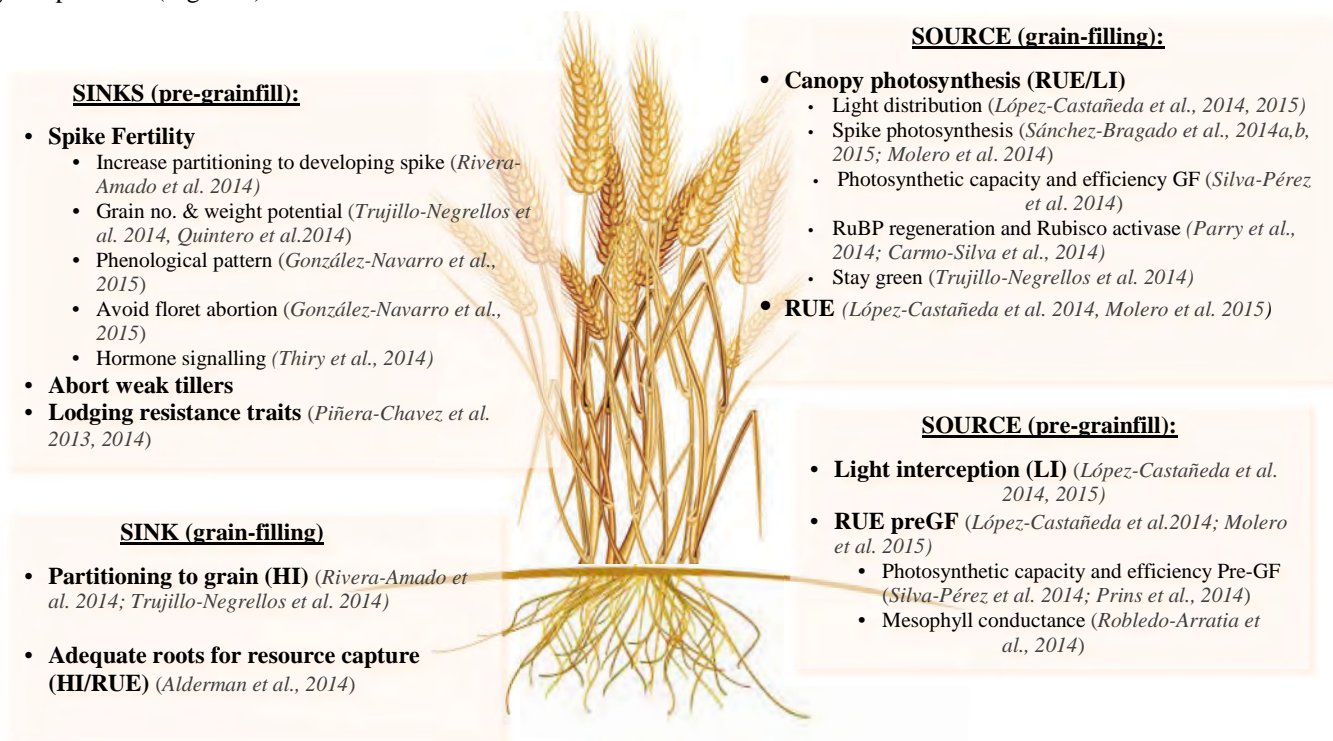**Figure 1. Traits studied in Wheat Yield Consortium to determine genetic variation in yield potential traits and for designing crosses that combine complementary yield potential traits in wheat (based on traits reviewed in Reynolds et al., 2011).** Traits are categorized as either net sources or sinks of photoassimilates, and their predominant expression is considered either before, during grain filling or both.

Summary of Results

Sixty elite lines of wheat, including the most advanced lines provided by CIMMYT breeders and some historical lines, were grown under yield potential conditions in the Mexican Phenotyping Platform (MEXPLAT), Ciudad Obregon, Sonora, Mexico for two seasons (2010-11 and 2011-12) and a subset of thirty lines (CIMCOG-Subset) were grown for another additional season (2012-13). The subset of 30 lines represented the genetic variability of the whole CIMCOG panel and was used for further analysis.

Radiation use efficiency (RUE) was dissected according to aboveground biomass harvested at different times during the growth cycle (Figure 2). Genotypic variation for RUE among the lines was observed (data not shown) with the exception of RUE comprised between initiation of booting and seven days after anthesis (RUE_{T3-T2}). The most important periods to determine final aboveground biomass were RUE from canopy closure (forty days after anthesis) to initiation of booting (RUE_{T2-T1}) together with RUE during grain filling (seven days after anthesis to physiological maturity, RUE_{GF}). In addition, RUE_{GF} appeared to be closely and positively associated with yield and thousand grain weight highlighting the importance of post-anthesis photosynthesis to determine final grain yield. The positive correlation between grain yield and grain filling RUE highlights a higher efficiency of the crop to convert intercepted radiation into biomass after anthesis can affect the activity at the sink.

In order to achieve high final aboveground biomass (BMat) it is important to produce high biomass in earlier stages (Figure 2) avoiding the loss of fertile stems at the end of the crop (Figure 3a). The positive correlation between biomass measured at initiation of booting with grain number (GNO) together with a positive correlation with water soluble carbohydrates measured at heading ($P<0.05$, data not shown) highlights the importance of pre-anthesis photosynthesis to increase spike fertility. However, as has been previously reported, this investment in more grains is negatively correlated with final grain weight probably associated with a possible source or source-sink co-limitation during grain filling (Figure 2).
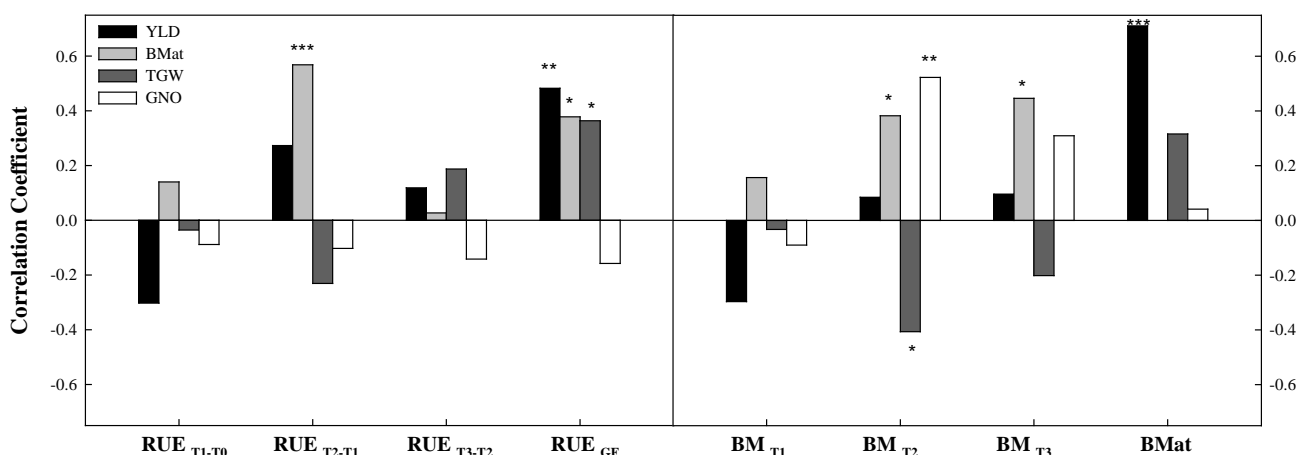

Figure 2. Phenotypic correlations between grain yield (YLD), aboveground biomass at maturity (BMat), thousand grain weight (TGW), number of grains per square meter (GNO) with radiation use efficiency (RUE) and biomass harvested at different times during the growth cycle: T0: emergence, T1: forty days after emergence, T2: initiation of booting, GS41, T3: seven days after anthesis, GS65+7, GF: grain filling,from GS65+7 until physiological maturity. ***$P<0.001$; **$P<0.01$; *$P<0.05$.

Even than under drought stressed conditions investments in early biomass is a desirable trait, no effect (or even negative) was observed under yield potential conditions (Figure 3a). Loss of spikes between seven days after anthesis until physiological maturity was negatively correlated with yield, biomass and radiation use efficiency suggesting than the ability to keep fertile stems during grain filling has a high impact on final yield. This ability is associated with higher RUE along the growth cycle (Figure 3a). The correlation of harvest index (HI) and other sink traits with yield and biomass highlights the importance of these traits to translate the extra biomass into grains (Figure 3b).
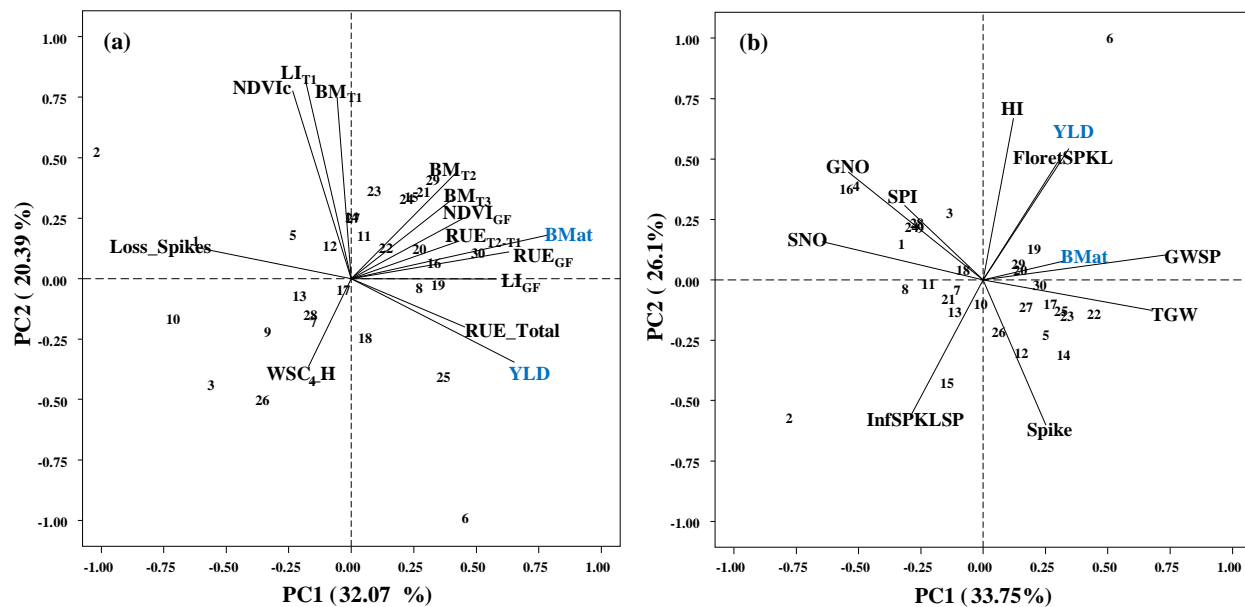
Figure 3. Principal component analysis of source (a) and sink (b) traits showing phenotypic (r_p) and/or genetic (r_g) correlation with yield (YLD) or aboveground biomass at maturity (BMat) for 30 genotypes of CIMCOG-Subset grown for three years in NW Mexico. Grains per square meter (GNO) did not correlated with YLD or BMat but is shown in the figure (b). Biomass measured 40 days after emergence (BME_{T1}), at initiation of booting (BM_{T2}) and seven days after anthesis (BM_{T3}), light intercepted 40 days after emergence (LI_{T1}) or during grain filling (LI_{GF}), radiation use efficiency from 40 days after emergence until physiological maturity (RUE_Total), from 40 days after emergence to initiation of booting (RUE_{T2-T1}), and from seven days after anthesis until physiological maturity (RUE_{GF}), normalized difference vegetation index at canopy closure (NDVIc) and during grain filling ($NDVI_{GF}$), water soluble carbohydrates in the stems at heading (WSC_H), loss of spikes between seven days after anthesis until physiological maturity (Loss_Spikes), harvest index (HI), thousand grain weight (TGW), grains per square meter (GNO), spikes per square meter (SNO), grain number per spike (GSP), spike index (SPI), number of infertile spikelets per spike (Infertile SPKLSP), number of florets per spikelet (FloretSPKL), grain weight per spike (GWSP), spike length (Spike). Percentage of variability explained by each principal component (PC) is indicated in brackets in each axis of the biplot.

Implications for Yield Potential

Theoretical considerations suggest that wheat yield potential could be increased through the genetic improvement of radiation use efficiency (RUE). According to the results, the most influencing periods to increase final aboveground biomass are the ones comprised between canopy closure and initiation of booting and during grain filling. In this sense, further research should be focus on these critical periods in order to increase yield potential. In this sense, due to spikes intercept more than 30% of light during grain filling, further studies to estimate the contribution of spikes to canopy RUE must be assessed.

These results highlight the importance of RUE during crop growth in order to maximize yield potential. However, to achieve agronomic impacts, structural and reproductive aspects of the crop must be improved in parallel with RUE.

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Genetic Diversity of Light Interception Profiles in Modern Wheat Canopies

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Background

The ideal crop canopy maximizes interception of solar radiation throughout the crop cycle while optimizing the distribution of light. The latter is important because photosynthesis saturates at about half the intensity of direct sunlight. Hence the maximum rates of canopy photosynthesis are achieved by increasing the leaf area index to values typically above three, and arranging leaves in a more erect posture thereby reducing the proportion of leaves in a light saturated state and increasing light penetration. In fact light interception is generally above 95% for most wheat canopies in favourable environments and modern wheat canopies already have erect or semi-erectophile canopies (Araus et al. 1993). However, there may be scope for further genetic alteration of leaf posture, leaf size or density to alter the architecture and hence the in-canopy light characteristics which influences the extent and dynamics of light saturation (Murchie et al. 2009). An area of canopy photosynthesis that has not been addressed in breeding before is the potential to improve the contribution from spikes. Studies were conducted in genetically diverse elite high-yielding spring wheat genotypes to determine light extinction patterns.

Summary of Results

Former research work conducted at CENEB showed substantial genetic variation in biomass, total leaves area, number of stems per square meter, leaf area index (LAI), extinction coefficient (k) and light intercepted (LI) by the canopy in a combined analysis of 60 genotypes measured under flat and raised beds during 2010-2011 (Table 1). In general, higher values for all traits were observed under flat planting system (PS). However, the interaction G x PS was only significant for light intercepted and extinction coefficient (k). The obtained k values also presented a wide genetic variation in flat and raised beds, showing there is scope to reduce the proportion of incident radiant energy transmitted in to the soil surface beneath the canopy, and so increasing LI by the canopy, especially under raised beds (Table 1).

One of the major aspects to consider in a plant breeding program is the heritability (h^2) of useful plant traits present in the available genetic variability. In Table 1, we can observe from moderate to high heritability for all traits in each individual analysis. Heritability was moderate to high for the combined analysis among planting systems with the exception of light intercepted. This can be explained by the G x PS interaction.

Genetic variation in LI intercepted by the canopy and its distribution into spikes and top leaves determined in flat beds showed spikes, flag leaf, leaf 2 and the reminder was 1.4, 1.4, 2.0 and 1.9-fold, respectively (Table 2). This has also shown spikes, flag leaf and leaf 2 intercepted more than 80 % of the above canopy incident radiation, and this also allowed us to establish that a longer peduncle and a longer internode between flag leaf and leaf 1 are key morphological traits to permit a greater penetration of light in to lower green leaves (López-Castañeda et al., 2014).

Table 1. Biomass measured seven days after anthesis (A+7), total leaves area, number of stems per square meter measured at A+7, leaf area index (LAI), light intercepted by the canopy and extinction coefficient, in flat and raised beds of CIMCOG genotypes during the winter-spring 2010-2011 in Cd. Obregón, Sonora, México. Broad sense heritability (h^2) for individual and combined analysis are shown in the table. All the traits in the table were measured seven days after anthesis.

| Trait | Flat beds | h^2 | Raised beds | h^2 | Combined Across Planting Systems (PS) | | | |
					Genotype (G)	Planting system (PS)	G x PS	h^2
Biomass A+7 (g m^{-2})	1085 - 1594	0.43	924 - 1438	0.487	**	*	ns	0.603
Total leaves area (cm^2)	84 - 156	0.784	73 - 149	0.741	***	ns	ns	0.818
Stems m^{-2} A+7	351 – 671	0.748	299 - 562	0.832	***	**	ns	0.831
LAI	3.9 - 7.5	0.601	3.4 - 5.9	0.532	***	*	ns	0.422
Light intercepted (%)	94.3 - 98.3	0.615	68.0 - 93.0	0.739	***	**	***	0.058
Extinction coefficient	0.42 - 0.93	0.506	0.22 - 0.65	0.624	**	*	**	0.320

According to heritability, in this case, k values had a high value for h^2, LI intercepted by spikes and LI intercepted by the rest of the canopy, had moderate h^2 values while flag leaf and leaf 2 presented low heritability values (Table 2).

Table 2. Adjusted mean, minimum and maximum values for a combined analysis of raised beds measured during 2011-2012 and 2012-2013 in a subset of 30 genotypes from *CIMCOG I*. All the variables were measured seven days after anthesis. Extinction coefficient (k) was calculated using leaf area index (LAI) and extinction coefficient with spikes (k_{SP}) was calculated using green area index (GAI, leaves and spikes). Light interception (LI) was measured at different *strata* of the canopy. Broad sense heritability (h^2) for combined analysis is shown in the table.

Variables		Mean	Min.	Max.	Genotype (G)	Year (Y)	G x Y	h^2
Leaf Area Index	*LAI*	5.5	4.5	6.4	**	*ns*	*	0.242
Green Area Index*	*GAI*	6.3	5.2	7.4	**	*ns*	*	0.262
Extinction Coefficient	*k*	0.48	0.32	0.65	**	*ns*	*	0.448
Extinction Coefficient with Spikes	k_{SP}	0.41	0.29	0.55	**	*ns*	*	0.447
LI (%)	LI$_{Spikes}$	32.6	24.8	41.1	*	*ns*	*ns*	0.385
	LI$_{Flag}$	29.7	19.3	38.0	*	*ns*	*	0.060
	LI$_{Leaf2}$	20.6	14.1	29.2	*	*ns*	*	0.117
	LI$_R$	6.8	2.0	12.5	**	*ns*	*ns*	0.641

*includes all green leaves and spikes

Implications for Yield Potential

The identification of key genetic and physiological factors that may help increase LI and reduce the transmission of radiation into the soil surface beneath the crop canopy, might offer good opportunities to increase yield potential through an increase in dry matter accumulation. A larger LI by spikes can be achieved by an increased spike size, which in turn may lead to an increased sink strength (e.g., grain number and size) and a greater partition of assimilates to the grain during the grain filling period. So, that selection by higher spike LI and lower k values may result in an increase in dry matter production and grain yield. A good example of success in a significant reduction of k values is given by Monteith (1965) and Cooper et al. (1983); these authors showed k to have values between 0.3 and 0.5 and 0.37 respectively, which are higher than the k values obtained in the present research work (mean of k=0.23). The substantial reduction in the k values observed in these studies (≈ 60 %) as compared with the mean of k values obtained by Monteith (1965) and Cooper et al. (1983) represent a clear example of progress achieved through unconscious selection leading to a significant reduction in the proportion of radiant energy transmitted to the soil surface beneath the crop canopy.

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Design Guided Engineering Higher Canopy Photosynthetic Light Use Efficiency

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In the past few years, we have designed systems model of canopy photosynthesis and canopy photosynthesis measured systems, which makes it now possible to systematically investigate possible options to improve canopy photosynthetic efficiency. The canopy photosynthesis model that we have developed includes both a realistic presentation of canopy architecture and also the photosynthetic characteristics. With such a model, we showed that the previous models without considering the detailed light heterogeneity can introduce up to 17% bias in the estimates of canopy photosynthesis rate. The new model has been used to explore the idea architecture of a crop canopy under elevated CO_2 conditions. We also used it to explore the consequences of manipulating photosynthetic antenna size on canopy light and nitrogen use efficiency. Recently, it is used to explore the consequences of changing the agronomic practices on canopy photosynthetic efficiency. These applications represent new systems to model canopy photosynthesis.

New temperature response parameters for wheat Rubisco

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Background

In order to select for improved photosynthesis, it is first necessary to identify genetic variation. The photosynthetic rate of an unstressed young leaf under high light and ambient CO_2 reflects, firstly, the underlying content and characteristics of photosynthetic enzymes and, secondly, the ease with which CO_2 can reach the sites of carboxylation from the atmosphere. The first constraint is related to the nitrogen content per unit leaf area, its allocation to photosynthetic enzymes such as Rubisco and the kinetic properties of the enzymes. The second constraint is associated with stomatal and mesophyll conductances. By analyzing gas exchange data with the standard Farquhar, von Caemmerer and Berry C_3 photosynthesis model (Von Caemmerer and Farquhar 1981), it is possible to identify the underlying components that are associated with variation in the measured photosynthetic rate. However, to measure a sufficiently detailed CO_2 response curve in the field requires about 30 minutes limiting how many genotypes can be screened. We have been developing a higher throughput method for assessing photosynthetic properties of wheat leaves using reflectance spectra. This was calibrated in the field against CO_2 response curves measured with conventional gas exchange. While the LI6400 is able to control leaf temperature to some extent, it was not always possible to achieve a common temperature of 25 C in the field (especially when ambient temperature was above 30 C combined with high irradiance). In fact, leaf temperatures for the experiments conducted in Australia and Mexico ranged between 20 and 34 C. Checks were made by repeated measurement of several leaves through a day at different temperatures. When the standard Farquhar, von Caemmerer and Berry C_3 photosynthesis model was applied, we found that the derived Rubisco activity corrected to 25 C was not constant. This prompted us to conduct an experiment where CO_2 response curves were measured repeatedly with the same leaf over a range of temperatures. From these measurements, we have derived a set of activation energies and values for Rubisco kinetic parameters at 25 C.

Summary of Results

Here, we will focus solely on the Rubisco limited region of CO_2 response curves. The equation describing this contains the following parameters: V_{cmax}, the maximum Rubisco carboxylase activity per unit leaf area (at 25C), Γ_*, the CO_2 compensation point in the absence of day respiration, R, (non-photorespiratory mitochondrial respiration), and K_c and K_o, the Rubisco Michaelis-Menten constants for CO_2 and O_2. Each of these parameters varies with temperature, which can be described by an activation energy, E_a. To fit the Rubisco limited equation, one also needs to know C and O, the partial pressures of CO_2 and O_2 at the sites of carboxylation. Kinetic constants for wheat have been determined in vitro (e.g. Makino et al. 1988, Cousins et al. 2010, Galmes et al. 2014, Carmo Silva et al. 2010) but there is considerable variation and their activation energies are lacking. For tobacco, a complete set of kinetic parameter values which includes activation energies has been derived in vivo from gas exchange measurements (Bernacchi et al. 2002). When we applied these to field data where leaves were repeatedly measured through a day at different temperatures, we observed that the V_{cmax} values deviated from the expected relationship above 28 C (Figure 1).
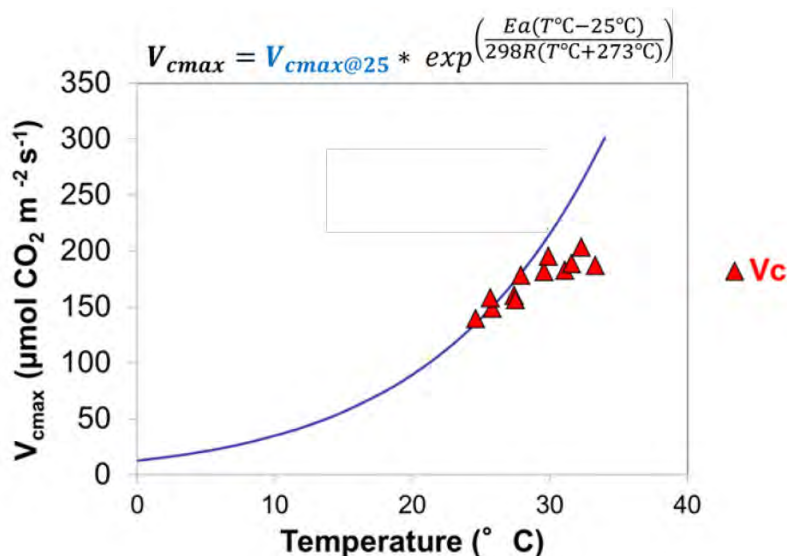

$$V_{cmax} = V_{cmax@25} * exp^{\left(\frac{Ea(T°C-25°C)}{298R(T°C+273°C)}\right)}$$

Figure 1. Example of V_{cmax} derived from a wheat leaf measured at different temperatures. The blue curve is the theoretical expectation (equation shown above) using kinetic parameters from Bernacchi et al. (2002).

Consequently, an experiment was performed using greenhouse grown plants which were transferred into a growth cabinet where leaves were repeatedly measured at 15, 20, 25, 30 and 35 C. In order to better constrain the analysis, curves were measured under both 2 and 21% O_2. Separate experiments measuring mesophyll conductance on these wheat cultivars (Estavillo et al. unpublished, 0.55 mol m^{-2} s^{-1} bar^{-1}) were conducted and we assumed the temperature response of mesophyll conductance determined for *Triticum aestivum* cv Yecora 70 (von Caemmerer and Evans 2014). We assumed the values at 25 C for K_c, K_o and Γ_* and the activation energy for R from Bernacchi et al. (2002) and derived an activation energy for V_{cmax} from Evans (1986). For each leaf, the multiple curves were then fitted to single values for V_{cmax} and R at 25 C and activation energies for K_c and K_o were found (Figure 2).
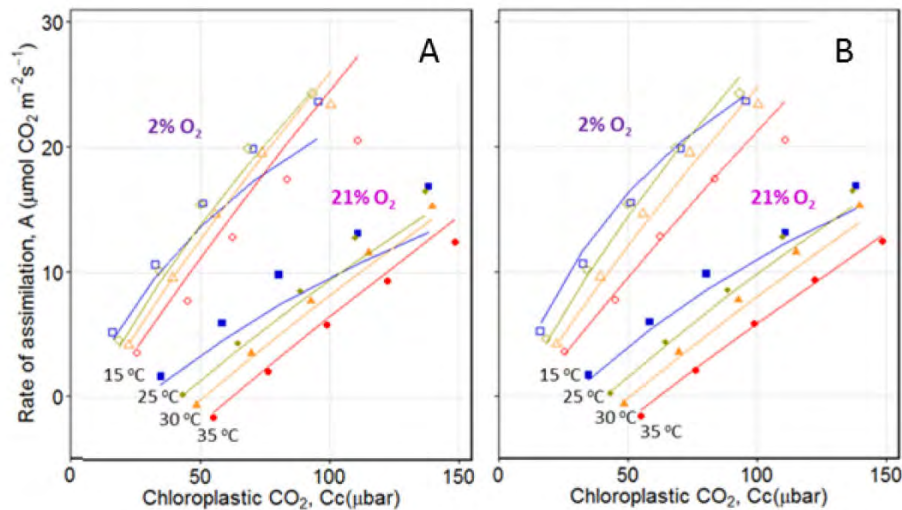

Figure 2. Example set of CO_2 response curves measured on one leaf at four different leaf temperatures in 2 or 21% O_2. A, curves are the fitted model using kinetic constants from Bernacchi et al. (2002). B, different activation energies for V_{cmax}, K_c and K_o have been assumed for the model curves which result in an improved fit.

Improved agreement between observed gas exchange data and model predictions was achieved by varying the activation energy assumed for K_c and K_o, while retaining all the other parameter values that had been derived for tobacco in vivo. Mean values for these activation energies were then applied to the analysis of three other wheat varieties and one triticale that were grown in the greenhouse but only measured in 21% O_2. Estimates of V_{cmax} were derived for each leaf at each temperature and converted to 25 C. Whereas $V_{cmax@25}$ declined by 30% from a leaf measured at 15 C to one at 35 C when the activation energies from Bernacchi et al. (2002) were used, with the newly derived activation energies, the decline varied between 5 and 15% over that same range. There was no indication that different values would need to be assumed for particular cultivars. The new activation energies were then applied to the analysis of data collected in the field and we observed that the derived estimate of $V_{cmax@25}$ was less dependent on the leaf temperature at the time of measurement.

Implications for Yield Potential

The newly derived activation energies now enable us to analyse the field data we have collected where we had been unable to maintain leaf temperature at 25 C. We will have greater confidence in the estimates of $V_{cmax@25}$ which in turn will improve our ability to calibrate the leaf reflectance method. Due to the speed with which reflectance measurements can be made, this method should allow extensive screening of wheat lines under field conditions. In turn, this will enable us to identify suitable parents to set up recombinant inbred line populations that are needed to hone in on the genetic basis for variation in photosynthesis.

Variation in Rubisco activity at temperatures around 35 C could arise from several different causes. First, while Arrhenius temperature response functions are assumed to apply to both Michaelis-Menten constants and catalytic rate constants, there are hints that a single activation energy may not hold over the full range of temperatures commonly experienced by wheat leaves in the field (Badger and Collatz 1977). Second, it has also been suggested that the activation state of Rubisco could vary with temperature as a result of declining Rubisco activase activity at higher temperatures (Carmo-Silva and Salvucci 2011; Parry et al. 2013). Third, there is evidence that the kinetic parameters of Rubisco vary between

species (e.g. Yeoh et al. 1980; Galmes et al. 2014). Consequently, without further detailed biochemical examination, variation in $V_{cmax@25}$ derived from gas exchange may not truly represent the underlying cause of variation in photosynthetic rate and this could lead to problems identifying the genetic basis.

There are several different possible routes for altering photosynthetic properties which could lead to increased yield potential. Photosynthetic rate can be increased by raising the photosynthetic capacity of the leaf. This could come about because the leaf has a greater nitrogen content and therefore more photosynthetic proteins per unit leaf area. Alternatively, the leaf could alter the internal allocation of nitrogen which could increase Rubisco content at the expense of some other leaf protein(s). Another possibility is that a Rubisco with kinetic properties superior to existing wheat lines could be identified from wheat germplasm collections or wild relatives and used to replace the current form. It is this last option that has the greatest potential to increase yield with the least requirement for additional nitrogen. Justifiably, attention is focused on Rubisco as under normal field conditions, this enzyme has been demonstrated to determine photosynthetic rate and it accounts for such a large fraction of leaf nitrogen.

The objective of this research has been to develop a more rapid methodology to screen photosynthetic characters, either in the field or grown in controlled environments. We are now in a position to apply this technique to screen a larger number of genotypes. First, we need to characterise parents of existing recombinant inbred line populations to identify those suitable for detailed screening. A broader screen of elite genotypes is also needed as this may identify better potential parents for new RIL populations. Screening of these populations will then allow the discovery of markers and the genetic basis for the variation in photosynthetic characters. This in turn will enable the identification of parents that can be used in a breeding program to enhance photosynthesis and provide markers that can assist in selection.

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Targeting TOR Signaling to Improve Performance in Crop Plants

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Background

Performance in a crop context is influenced by many factors, and advancing the understanding of underlying mechanisms will provide new approaches and gene targets for improving productivity in crops. Since Target Of Rapamycin (TOR) signaling regulates essential functions associated with cell growth, development, protein synthesis and cellular metabolism –- it holds important clues to similar functions in plants with potential implications to plant performance. The major component of this signaling is TOR protein kinase, highly conserved in eukaryotes from yeast to animals and plants. However, the functions of TOR signaling in plants are largely unknown. To address the functions of TOR in plants, we performed detailed developmental, physiological, genetic and molecular studies using model plant species Arabidopsis, crop species canola and more recently wheat.

Summary of results

We have isolated full length cDNA (~7.5 kb) and genomic clones of very large TOR encoding genes from Arabidopsis, Brassica, Brachypodium and wheat. The protein coding regions of these show high similarity suggesting their conservation and likely involved in similar functions. We have developed loss and gain of function along with conditional repression lines in Arabidopsis. Our studies showed that TOR is an essential gene and required for embryonic and postembryonic development. Further, the genetic, physiological, trancriptome and metabolome studies revealed that TOR functions areassociated with translation, carbon and nitrogen metabolism, nutrition, light energy with implications for photosynthesis and lifespan. Our canola studies revealed similar functions for TOR in development, and additionally with activated TOR expression – we observed fast growth, increased biomass, and early completion of crop cycle under field conditions. To explore similar applied possibilities for TOR signaling in wheat, recently we initiated functional studies using TOR homologs isolated from Brachypodium and wheat. Preliminary results from these studies suggest TOR functions in growth, development, light signaling and stress response pathways – detailed studies on these are in progress.

Implications on wheat yield potential

Advancing critical knowledge for TOR signaling associated with growth, biomass, light and photosynthesis could potentially lead to development of new strategies to improve performance and yields in wheat crop.

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Photosynthetic Contribution of Ear to Grain Filling in Wheat: Comparison of Different Methodologies for Evaluation

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Background

There is an increasing necessity in raising wheat yield potential and stability (Reynolds & Borlaug 2006; Araus *et al.* 2008; Reynolds *et al.* 2011) is increasing in view of the growing challenges imposed by social and climate changes. Moreover, genetic advances fuelled by breeding programs have decreased over recent decades (Reynolds et al. 1996; Araus et al. 2008). There is a need to develop more efficient wheat breeding methodologies, particularly phenotyping strategies, which complement existing (traditional) breeding techniques (Araus et al., 2008). One of the approaches proposed to increase yield potential and improve adaptation to abiotic stresses, such as drought and heat, is to select for higher ear photosynthesis. Hence, ear photosynthesis is thought to play an important role in terms of the source of photo-assimilates during grain filling, not only under drought, but also under good agronomical conditions (Araus et al. 1993; Bort et al. 1994; Abbad et al. 2004). Although the photosynthetic contribution of the ear to final grain weight has been widely studied (Araus et al. 1993; Bort et al. 1994; Tambussi et al. 2005, 2007; Maydup et al. 2010; Saeidi et al. 2012), its actual importance in terms of contribution to grain filling is not well understood (Tambussi et al. 2007), which has prevented the settling down of high-throughput phenotyping approaches for this trait. The main objective of this work was to compare different experimental approaches aiming to assess the relative photosynthetic contribution of the ear and the rest of the plant (the culm) to grain filling. Three different techniques were used: inhibition of ear and culm photosynthesis through i) herbicide DCMU application; or ii) by shading each organ; and iii) a non-disturbing approach which compares the carbon isotope composition (δ^{13}C) in its natural abundance of assimilates from different plant parts (awns and peduncle) with the δ^{13}C of the mature grains. Several advanced CIMMYT lines were tested under good agronomic conditions.

Summary of Results

Our results from the shading treatments indicate that total photosynthetic contribution of the ear represents 60% of total assimilates going to the grain (Figure 1). Conversely, the DCMU approach assigned a higher role to the culm photosynthesis, but herbicide application in the culm affected the ear, biasing the final grain weight. Nevertheless, results from any treatment of intrusive nature should be interpreted with caution, as unwanted compensatory mechanisms in the remaining unaffected organs could affect final grain weight.

In the approach using δ^{13}C, the relative contribution of awns to grain filling was also higher compared to the culm, although it depended on water status (assesses through $\delta^{13}C_{grains}$) and the overall similarity of magnitude than the value inferred from the shading approach. Thus, ear photosynthesis (awns) represented on average 60% of the total assimilates going to the grain, and up to 87% when water conditions were less optimal in the most positive interval of the $\delta^{13}C_{grains}$ (-25.0, -26.0 ‰).

Ear contribution to grain filling may yet be underestimated since the glumes were not included in the approach using δ^{13}C. Using the δ^{13}C approach, we provide a precise tool for assessing the photosynthetic contribution of the ear to grain filling, which can help design crosses to breed new lines adapted to a wide range of environments. However, some considerations should be taken into account in order to apply the δ^{13}C approach, such as the sampling methods, avoiding post-harvest respiration.

Implications for Yield Potential

In accordance with the results obtained in this study using different approaches, under good agronomical conditions the contribution of the ear to filling grains was comparable or even higher to that of the rest of the plant. Even under good agronomical conditions ear photosynthesis plays a key role as a source of photo-assimilates during grain filling. This trait has to be incorporated into conceptual models addressing wheat yield potential. Moreover our study advances the development of high-throughput phenotyping tools to assess ear contribution to grain filling. This study may help develop precise phenotyping tools to identify physiological traits such as ear photosynthesis that could contribute to increased grain yield. As far as we know, this is the first report where different experimental approaches of an intrusive and non-intrusive nature, aiming to assess the contribution of ear photosynthesis to grain filling were compared.
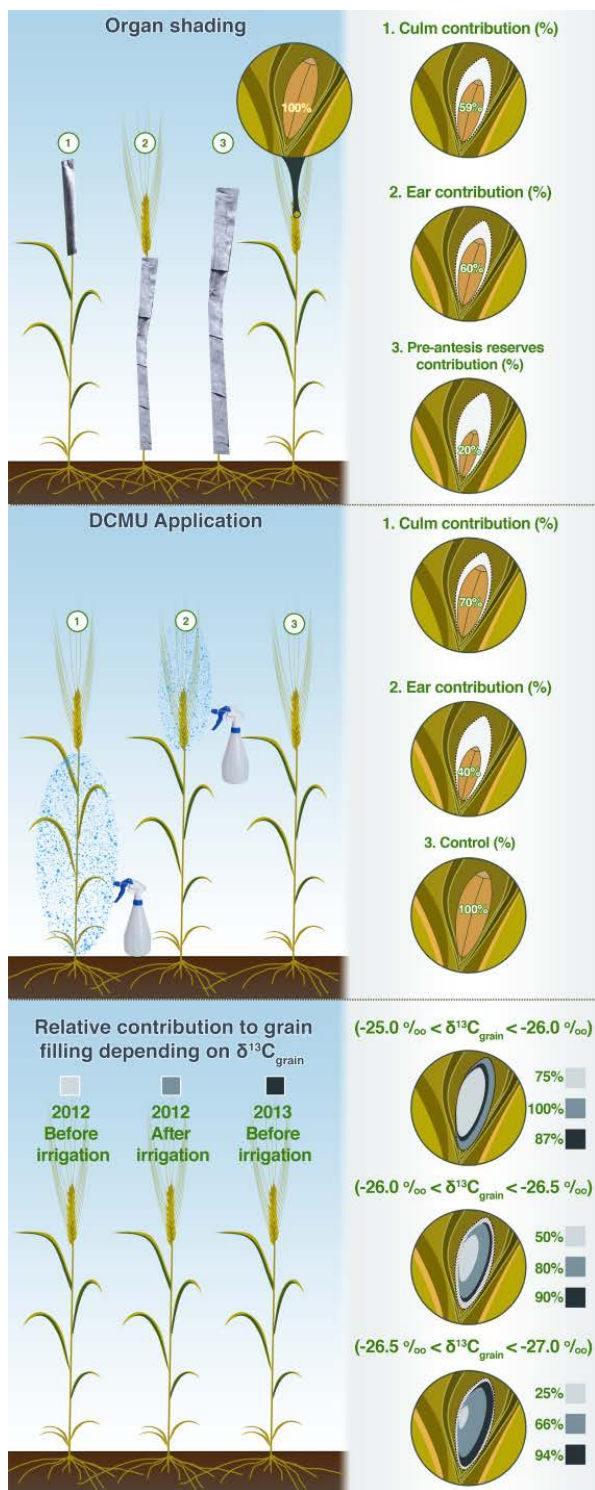
Figure 1. Illustration of a wheat plant showing the relative photosynthetic contributions of the ear and culm to grain filling estimated using the three different methodologies compared in this study.

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Discovery and Creation of Genetic Variation to Enhance Photosynthesis and Yield

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Background

Photosynthesis is the primary determinant of biomass with more than 90% of biomass (on a dry weight basis) derived directly from photosynthetic products. There is compelling evidence from free air CO_2 enrichment experiments (FACE) that increasing photosynthesis does increase crop yields provided that other constraints do not become limiting (Ainsworth & Long, 2005). The maximum theoretical efficiency with which the sun's energy can be captured as crop biomass is 4.5 to 6%, although it seldom exceeds 2% and averages less than 1%. Improving this conversion efficiency is an important area of research, with the potential to significantly increase crop yields. The processes underlying photosynthesis are highly conserved in different species and thus progress that is made in a model species should equally apply to crop species (Parry *et al.*, 2011; 2013; Carmo Silva *et al.*, 2014).

One of the reasons for low photosynthetic efficiency (e.g. of rice and wheat) is that the primary carboxylating enzyme, ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco), is slow and also catalyses a competing reaction with O_2 rather than CO_2. Much research has focused on overcoming the limitations of Rubisco either through mining natural diversity (Driever et al 2014) or by genetic engineering (Lin et al 2014a; 2014b), and has included attempts to increase the flux of CO_2 to the site of utilisation by Rubisco. Significant progress has also been made toward promoting a plentiful supply of the CO_2 acceptor molecule and Rubisco co-substrate, ribulose-1,5-bisphosphate (RuBP), through altered expression of rate-limiting enzymes required for its continuous regeneration.

Summary of Results

The concentration of CO_2 at the catalytic site of Rubisco is a major determinant of photosynthetic rate and is strongly influenced by both the stomatal conductance (g_s) and the mesophyll conductance (g_m). Differences in physical characteristics lead to the large variation in g_m among species (Flexas *et al.*, 2012). One goal was to determine the extent of variation in g_m between wheat cultivars.

The photosynthetic performance of 13 field-grown cultivars of *Triticum aestivum* (bread wheat) at the CIMMYT experimental station in Sonora, Mexico, was screened using gas exchange and fluorescence equipment. Mesophyll conductance (g_m) was highly variable even between cultivars of wheat (Fig. 1). Leaf age and water availability were carefully controlled to eliminate their impact on the observed variation in g_m, for which reason the observed differences must have been inherent to the cultivars themselves, probably reflecting distinct anatomical characteristics.
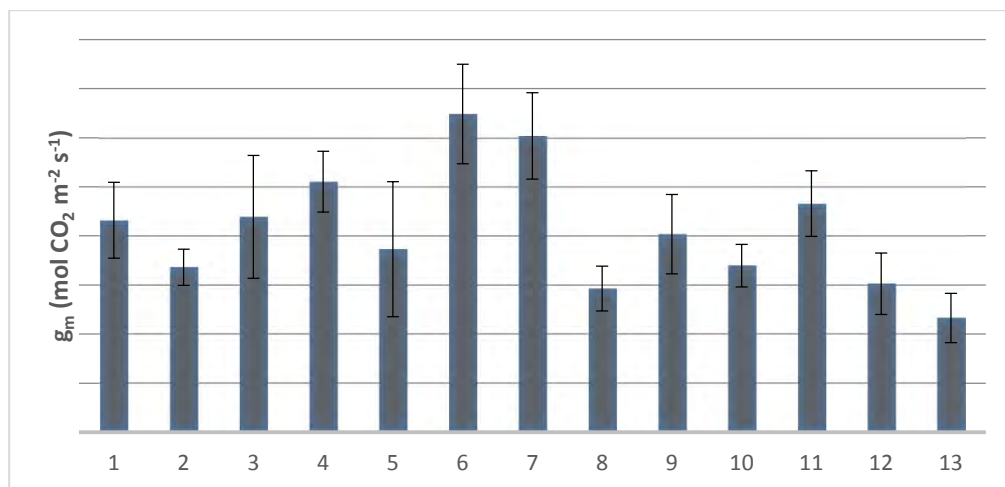

Fig. 1. Mesophyll conductance (g_m) of 13 wheat varieties grown in the field, at CIMMYT.

There is natural variation in the catalytic properties of Rubisco isolated from various higher plants (see e.g. Galmés *et al.*; 2005, 2014*a*; 2014*b*; Andralojc *et al*., 2014). We have determined the natural variation of Rubisco catalytic properties in a range of closely related species in the Triticeae tribe. Genotypes that evolved in different climates were selected to identify forms of Rubisco with superior kinetic properties to those found in *Triticum aestivum* (bread wheat). The newly available catalytic parameters were assessed *in silico* using a biochemical model of leaf photosynthesis (Figure 2). This approach suggested that Rubisco from several of the genotypes could outperform the native bread wheat enzyme. These traits can be harnessed either through wide crosses (conventional breeding) or by molecular techniques to improve the photosynthetic capacity and yield potential of wheat.
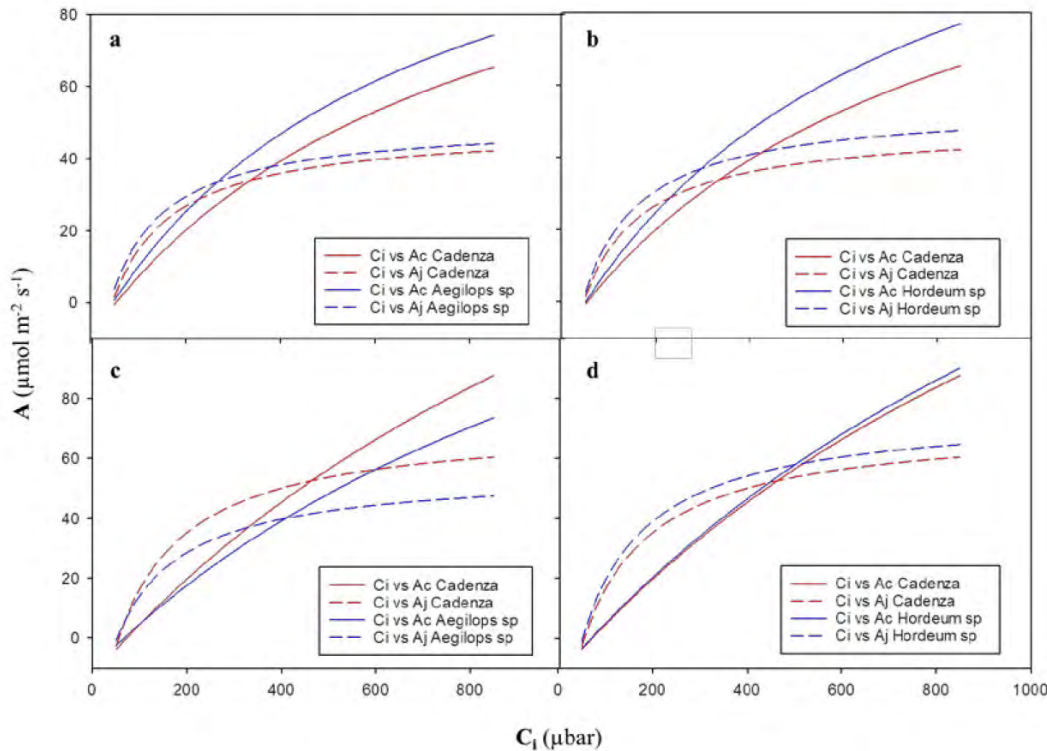

Fig. 2. Modelling photosynthesis at 25°C (a, b) and 35°C (c, d), to demonstrate the effects of replacing the Rubisco of *T. aestivum* cv Cadenza (red) with Rubisco from (a, c) an *Aegilops* candidate or (b, d) a *Hordeum* candidate (blue). The Rubisco-limited (Ac, solid lines) and RuBP-regeneration-limited (Aj, dashed lines) rates of net CO_2 assimilation (A) were derived using the model ofFarquhar et al. (1980) and the Rubisco catalytic constants as measured for each genotype in separate experiments.

Photosynthesis is co-limited in the canopy by the kinetics of Rubisco on the one hand, and the regeneration rate of RuBP on the other. Increasing RuBP regeneration in model plant species by overexpressing rate limiting enzymes involved in RuBP regeneration (sedoheptulose-1,7-bisphosphatase (SBPase) and fructose-1,6-bisphosphate aldolase (FBP aldolase)) substantially increases photosynthesis (e.g. Lefebvre et al. 2005). Whether or not the improved supply of RuBP can alone increase photosynthesis in wheat, the co-limitation of photosynthesis implies that improvement in both limiting processes (RuBP regeneration and Rubisco catalyzed carboxylation) will ultimately be called for.

The common UK wheat cultivar Cadenza and the CIMMYT lines HIST10 and HIST13 were genetically modified to overexpress SBPase or FBP aldolase in the choroplast. The presence of the SBPase or FBP aldolase transgenes were verified by PCR analyses. Gene expression levels and protein amounts in plants harboring the foreign DNA are being determined by RT-qPCR and Western Blotting. Photosynthetic performance is being measured by the response of net CO_2 assimilation (A) to the intercellular CO_2 concentration (Ci) using an infra-red gas analyser (LiCor, LI-6400XT). Increased protein expression has been confirmed in first and second generation (pSBPaseTa1&2 and pFBPaldolaseTa1&2) transformants. Preliminary data for isolated plants suggest increased photosynthetic performance and biomass in plants with increased levels of SBPase (Figure 3), although no significant effects accompanied increased levels of FBPaldolase

Fig 3. Glasshouse grown control and transgenic wheat lines overexpressing SBPase.

Implications for Yield Potential

We have identified substantial variation in several important photosynthetic components, including g_s and g_m, between genotypes from germplasm collections. Thus, molecular genetic approaches combining sequence information and genotype can be expected reveal new molecular markers for breeding.

We have identified variation in Rubisco kinetics that could be exploited by wide crossing or genetic manipulation. Given the technical obstacles relating to the transformation of cereal chloroplasts, the GM route is not yet straightforward.

Increasing SBPase expression appears to increase the biomass of individual plants. We now need to establish whether this is robust under a wider range of conditions, particularly within closed canopies.

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