

Exploring genetic diversity for biomass and traits related to canopy photosynthesis

The ultimate frontier for raising yield potential of crops is to improve photosynthetic capacity and efficiency. While theory suggests that radiation use efficiency (RUE) of wheat and other C3 crops can be improved by at least 50%, this will require considerable research focused at cellular and sub-cellular processes (Zhu et al., 2010). In the meantime, three near-term approaches can be employed to boost yield potential.

1. Increasing crop biomass by tapping into genetic resources that express favorable growth rate.
2. Increasing RUE by increasing sink-demand for assimilates.
3. Stabilizing and increasing expression of harvest index.

This project focuses on 1), namely increasing crop biomass by tapping into genetic resources, the complementary approaches 2) and 3) are described in parallel proposals.

Evidence for genetic diversity

While biomass of elite cultivars has increased modestly in recent years (Shearman et al. 2005; Aisawa et al., 2015), genetic resource screenings have identified biomass values well over those expressed in the best modern cultivars (Reynolds et al. 2015). For example, Table 1 shows data from a set of primary synthetic lines that were evaluated under yield potential conditions in Mexico, with the best line showing 23% more biomass than the check.

Table 1. Ten primary synthetics showing highest biomass from replicated yield trials of 100 pre-selected lines, NW Mexico 2011

Primary Synthetic Cross	Yield Maturity		Biomass	Norm Biom*	% of check Biom*
	g/m ²	days	g/m ²	g/m ²	(%)
CETA/AE.SQUARROSA (166)	585	120	1981	2036	123
68.111/RGB-U//WARD/3/FGO/4/RABI/5/AE.SQUARROSA (778)	511	123	1909	1912	116
CROC_1/AE.SQUARROSA (213)	452	125	1902	1883	114
68.111/RGB-U//WARD/3/FGO/4/RABI/5/AE.SQUARROSA (788)	440	130	1975	1880	114
YAV79//DACK/RABI/3/SNIPE/4/AE.SQUARROSA (457)	475	128	1923	1860	113
68.111/RGB-U//WARD/3/FGO/4/RABI/5/AE.SQUARROSA (784)	612	117	1752	1841	111
D67.2/PARANA 66.270//AE.SQUARROSA (796)	616	119	1767	1833	111
D67.2/PARANA 66.270//AE.SQUARROSA (465)	626	119	1759	1823	110
GARZA/BOY//AE.SQUARROSA (281)	493	130	1912	1812	110
LCK59.61/AE.SQUARROSA (313)	455	130	1903	1811	110
Check (Sokoll)	681	117	1571	1656	100
MEAN	540	123.3	1850	1850	112
C.V.	9.00	0.75	6.75	-	-
LSD (5%)	83.9	1.84	223	-	-

*normalized to days to maturity

Biomass is a function of light interception (LI) and RUE integrated over the entire crop growth cycle. Under the MasAgro-TRIGO project, detailed growth analysis has shown genetic diversity for LI and RUE at different phenological stages, suggesting discrete genetic control (Table 2). This is important in terms of a pre-breeding strategy which through strategic hybridization could combine complementary alleles associated with favorable expression of LI and RUE identified at distinct growth stages from different genetic backgrounds.

In addition to growth rate *per se*, genetic diversity exists for a number of relatively simple canopy photosynthesis related traits that can contribute to improved RUE, including leaf canopy architecture (Murchie et al., 2009), distribution of chlorophyll throughout the canopy (Melis et al., 2009) and spike

photosynthesis (Tambussi et al. 2007). Furthermore, genetic diversity for Rubisco carboxylation capacity has very recently been determined using gas-exchange analysis in a diverse panel of 64 elite wheat cultivars grown in the field (Driever et al., 2014). These findings strongly support the case for significant underutilized photosynthetic capacity in existing wheat germplasm .

All of these traits will be explored in this project with the view to combing the best sources in pre-breeding to combine complementary alleles.

Table 2. Genetic variation for biomass, light interception (LI) and radiation use efficiency (RUE) at different growing stages in a set of 30 elite lines evaluated during 3 years in NW-Mexico (2011, 2012 and 2013). T0: emergence, T1: 40 days after emergence, T2: initiation of booting, T3: 7 days after anthesis, GF: grain filling.

	Mean	Min.	Max.	C.V.	Heritability	Gen	Year	Gen x Year
Biomass _{T1} (g m ⁻²)	169	146	192	8.04	0.54	***	ns	*
Biomass _{T2} (g m ⁻²)	634	499	848	6.03	0.90	***	**	**
Biomass _{T3} (g m ⁻²)	1120	950	1313	7.05	0.64	***	ns	**
Biomass _{GF} (g m ⁻²)	1425	1259	1525	3.51	0.78	***	*	*
LI _{T1} (%)	87.1	73.8	91.7	2.5	0.85	***	*	ns
LI _{T2} (%)	95.9	89.9	98.9	1.8	0.73	***	**	**
LI _{T3} (%)	94.7	89.1	97.7	2.2	0.51	***	*	*
LI _{GF} (%)	74.4	61.3	83.4	6.4	0.76	***	ns	ns
RUE _{T1-T0} (g MJ ⁻¹)	0.60	0.51	0.69	7.8	0.53	**	**	ns
RUE _{T2-T1} (g MJ ⁻¹)	1.89	1.63	2.13	6.7	0.54	**	**	ns
RUE _{T3-T2} (g MJ ⁻¹)	1.84	1.45	2.22	14.6	0.06	ns	**	ns
RUE _{GF} (g MJ ⁻¹)	0.75	0.47	1.02	23.1	0.30	*	ns	ns

State of the art of phenotyping and genotyping.

There is clear evidence for expression of superior LI and RUE in genetic resources. Under the MasAgro-TRIGO project, genetic variation in elite lines was found to be significant at all growth stages studied (Table 2) and principal component analysis indicated that LI and RUE at the different growth stages are under discrete genetic control (Fig 1), indicating an opportunity to pyramid useful alleles.

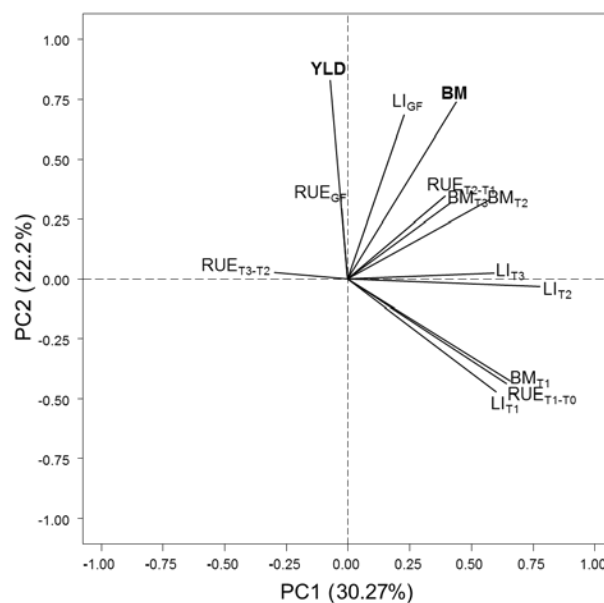


Figure 1. Biplot of source-related traits in 30 elite lines evaluated over 3 years in NW-Mexico. T0: emergence, T1: 40 days after emergence, T2: initiation of booting, T3: 7 days after anthesis, GF: grain filling.

Remote Sensing

It is not trivial to perform growth analysis on large numbers of lines; conventional growth analysis is not high throughput. A number of proximal and remote sensing (RS) protocols have been pioneered by CIMMYT's wheat physiology group over the last decade. For example, good associations have been demonstrated between the spectral indices NDVI and Water Index with in-season biomass (Babar et al., 2006). Using airborne platforms, biomass estimations can now be measured at higher throughput and with greater precision under a range of environmental conditions (Chapman et al., 2014; Tattaris et al., 2014). Therefore, growth analysis can be performed on relatively large numbers using RS approaches permitting expression of RUE at different growth stages to be effectively screened for.

In order to help identify lines with improved Rubisco carboxylation capacity and efficiency in the field, leaf hyperspectral methodologies are under development in collaboration between CIMMYT and Australian National University (Silva-Perez et al., 2014). The refinement of this methodology will complement other RS approaches for screening large numbers of lines in field conditions, with a specific focus on real-time photosynthesis. This could prove especially interesting for pinpointing lines that respond well to anomalous conditions such as heat waves or cloudy conditions, for example.

Canopy architecture

Despite a number of reviews that have highlighted the importance of canopy architecture in improving RUE in wheat and other crops (Murchie et al., 2009; Ort et al., 2015), there have been relatively few attempts to incorporate theoretically useful canopy traits into breeding, in spite of demonstrated genetic variation. One exception is that of erect leaf posture that was introduced from *T. timopheevii* into the CIMMYT spring wheat gene pool in the 1970s and can still be seen in some of the high yielding "Kauz" derived wheats, as well as in most CIMMYT durum lines (Fischer, 2007). Studies of canopy architecture have generally focused on leaf angle; however, there are other ways in which light extinction can be attenuated to improve the overall RUE of the whole crop canopy (Melis et al., 2009; López-Castañeda et al., 2015).

While the exact cause of light extinction is not straightforward to determine in terms of morphological traits, its effect is relatively easy to measure using light bars or ceptometers. Recently two additional canopy related traits have been proposed. One is the re-distribution of chlorophyll from higher to lower leaves (Melis et al., 2009), a trait which is relatively straightforward to measure at high throughput using the SPAD chlorophyll meter, as well as indirectly with ceptometers.

Another trait that has never been evaluated in a breeding context is spike photosynthesis (SP), which is surprising given that in a normal wheat canopy up to 40% of incident radiation—depending on genotype—is intercepted by the spikes alone (López-Castañeda et al., 2015). Spike photosynthesis contributes substantial carbon to grain filling (Tambussi et al. 2007; Sanchez-Bragado et al., 2014), shows genetic variation (Abbad et al. 2004; Molero et al., 2014), and the awns have an important role in diffusing and therefore optimizing light distribution through the canopy (Blum, 1985). The main bottleneck to improving SP in crops is that it is especially difficult to phenotype. However, different phenotyping approaches for measuring SP have been developed in the MasAgro-TRIGO project (Molero et al., 2013) and are being applied for screening of spring wheat panels.

Research Objectives and Methodology

The overarching goal of this project is to introduce sources of alleles that can contribute to the expression of a high final biomass and other contributing photosynthetic related traits into a range of elite genetic backgrounds. The specific objectives are:

1. Screen a diverse set of elite genetic resources for good expression of final biomass.
2. Characterize lines with high biomass for expression of LI and RUE at discrete growth stages in order to identify diverse alleles that contribute to high final biomass in complementary ways.
3. Evaluate diverse high biomass/RUE lines for canopy architecture traits that permit a more vertically uniform photosynthetic rate down the leaf canopy. These include leaf traits that permit more uniform light distribution (i.e. better light extinction), e.g. erectophile canopies, or a more optimal distribution of chlorophyll vertically.
4. Evaluate diverse high biomass/RUE lines for Rubisco capacity using high-throughput tools.
5. Pre-breeding to combine alleles for favorable LI and RUE together with other photosynthetic related traits in order to achieve high final biomass.

These objectives will be pursued through the following activities:

Germplasm exploration. The results outlined earlier (Table 2) indicating genetic variation for RUE even among selected elite lines, are very promising in terms of the likelihood of identifying other valuable genetic resources from a wider gene pool. The objectives above will be carried out on a number of spring wheat panels developed by CIMMYT's Wheat Physiology group in recent years (Appendix 1). One of the concerns of measuring large populations is the tendency for them to encompass a large range of phenology which can confound phenotypic and genetic analysis (Pinto et al., 2010). To overcome this problem, a number of these panels and mapping populations were developed or selected to restrict the range of phenology. In the other panels, experimental designs are used to block lines of different phenology classes.

Growth analysis. Diverse sets of spring wheat lines selected from a very broad base of genetic resources will be subject to growth analysis in representative high yield spring wheat growing environments at the IWYP platform in NW Mexico. In order to work with a sufficient volume of material, the initial screens will be performed using remote sensing, which will be performed at the following growth stages: (i) crop establishment (emergence to canopy closure), (ii) spike development (canopy closure until initiation of booting), (iii) rapid spike growth (initiation of booting until anthesis), and (iv) grainfilling (anthesis until physiological maturity). Promising subsets of lines will be selected for more detailed and precise growth analysis in subsequent cycles involving biomass harvests as well as direct estimates of light extinction.

Remote sensing to screen for Rubisco carboxylation capacity and photosynthetic efficiency of leaf canopies. Measurements of the photosynthetic capacity of the leaves in relation to Rubisco operational rates of CO₂ assimilation -per unit leaf area, and per unit leaf nitrogen (photosynthetic efficiency)- will be conducted on a subset of selected lines using a spectro-radiometer (ASD FieldSpec® 3 Full-Range 350-2500 nm) together with Kjeldahl digestion nitrogen analysis. Measurements will be made at different growth stages and under different daily conditions in order to pinpoint lines with favorable Rubisco dynamics under contrasting situations throughout the crop cycle.

Evaluation of canopy architecture. The canopy architecture traits will be measured initially on the same subsets of lines identified for expression of high final biomass. The traits include (i) erectophile canopies that can be assessed visually, (ii) better light penetration to lower depths of the canopy which will be assessed with a ceptometer, and (iii) more optimal vertical distribution of chlorophyll which will be measured with a SPAD meter. In subsequent cycles, a larger range of genetic resources will be examined for variation.

Pre-breeding. Pre-breeding will focus on two main approaches. Firstly lines identified by Objective 1 will be crossed with sources of good harvest index, while lines identified by Objectives 2, 3 and 4 will be used in strategic crosses among each other to combine different sources of LI and RUE with the idea to achieve cumulative gene action for biomass. Some of the same materials may be used in 3 way crosses to combine with good sources of harvest index.

Appendix 1. Panels and population available for biomass screening at the IWYP Platform

Primary Synthetics Diversity Panel (SynPan, 200 lines). CIMMYT has generated 2,000 so-called ‘synthetic wheat’ genotypes using novel genetic variation in diploid and tetraploid wheat. These primary synthetics can be crossed easily with elite bread wheat lines, and backcross derivatives are already well represented in new high yielding lines distributed by the International Wheat Improvement Network (IWIN). Field studies have also shown that synthetic-derived material can confer significant advantages in terms of yield and biomass under heat stress, a trait that may indicate superior Rubisco for example (Cossani and Reynolds 2015). Wheat Physiology recently screened all 2,000 lines under yield potential conditions as well as under heat and drought stress, and identified lines that expressed superior performance under each of these conditions as well as some in combination. A panel of 200 of the best primary synthetics has been assembled from screenings under high yield potential conditions. New synthetics will also be available in 2016 and beyond based on crosses of heat tolerant D and AB genomes that were screened in previous cycles for adaptation to high night temperature.

Progeny of Physiological Trait Crosses + Parents (PT+Pads) (~300 lines). CIMMYT has recently distributed -through the IWIN- a number of nurseries comprising novel elite germplasm designed to combine specific physiological traits associated with increased yield potential (1st to 3rd WYCYT, Wheat Yield Consortium Yield Trails), and adaptation to heat and drought (1st to 5th SATYN, Stress Adaptive Traits Yield Nursery). International trialing has identified lines with significant genetic gains over elite checks for both yield and biomass.

Wheat diversity panels. Association panels of selected wheat genetic resources (350 bread wheat; 200 durum wheat) have been assembled from spring wheat sources after screening approximately 60,000 lines for heat and drought adaption in the Sonoran desert. They were derived from the following sources:

- International nurseries. Every year approximately 1,000 new, high yielding, disease resistant wheat lines with appropriate end-use quality are generated by CIMMYT and delivered via IWIN to most public and private wheat improvement programs worldwide, where they are tested at approximately 200 sites annually. Now in its fifth decade, the IWIN database provides a valuable starting point to identify modern varieties with outstanding adaptive characteristics in specific environments (Braun et al., 2010; Gourdjji et al., 2012).
- Wheats with ancestral chromosomal introductions. Many elite lines already contain alien introgressions from the *Triticeae* tribe that are linked to improved yield potential and disease resistance (Ortiz et al., 2008). CIMMYT’s genebank holds around 500 accessions with specific translocations (e.g. 7Ag.7DL, 1B.1R, Lr34, Lr42), while thousands of elite lines are derived from crosses with synthetic wheat (see below).
- Landraces. Approximately 15,000 spring wheat landraces from the World Wheat Collection have recently been pre-screened under high temperature stress. Several hundred landraces were selected for superior yield and biomass (the latter evaluated visually).
- Focused Identification of Germplasm Strategy (FIGS) is landrace panel that have been selected based on their origin being in regions with abiotic stress (Sehgal et al., 2015).

High Biomass Association Panel (HiBAP). Systematic screening of genetic resources from the World Wheat Collection has identified genotypes with favorable expression of biomass. Approximately 150 spring types, including elite high yield material, pre-breeding lines crossed and selected for high yield and biomass, synthetic derived lines, and appropriate checks. The material has a restricted range of maturity to avoid confounding effects associated with extreme phenology.

Mapping Populations and Parents. Several populations (bi-parental, association mapping, genomic selection and NAM populations) are available at CIMMYT for the genetic dissection of complex traits. A number of suitable RILs populations are available whose parents are elite high yield/biomass lines, some of whose progeny express transgressive segregation for these traits while not expressing a large range of phenology. Some data already exists from previous projects for yield and NDVI at different growth stages which can be made available, and it is expected to phenotype at least two more populations depending on the demands put on IWYP-PLAT by successful projects. Among the extant populations, the most relevant include:

- CIMCOG: The panels of 60-100 lines represent a full range of genetic diversity in elite high yielding backgrounds and provide a common research platform for yield potential research. CIMCOG is renewed biennially using elite materials from various sources. The 1st CIMCOG has already been evaluated at 25 international sites in Asia and Africa, as well as at in different Mexican environments (Chavez et al. 2013).
- The WAMI panel consisting of 287 genetically diverse elite lines previously released by IWIN, was selected for a restricted maturity class to avoid confounding the expression of yield potential traits with phenology. WAMI has been mapped and genetic analyses have been conducted under high yield conditions (Lopes et al. 2015; Sukumaran et al., 2015). Further genetic analyses are pending using phenotypic data from almost 31 international environments (to date) making this a valuable resource for extrapolating research results to target wheat growing regions.
- The Kauz/Weebil double haploid population combines yield potential traits to generate lines with exceptional yield potential compared to either parent, as recently shown in southern Chile (Bustos et al. 2013).

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