Exploring genetic diversity for grain partitioning traits to enhance yield in a high biomass spring wheat panel

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Abstract

16 Breeding to raise yield potential through enhancing photosynthesis will have limited

17 impact unless harvest index (HI: proportion of above-ground biomass as grain yield)

18 is maintained or ideally increased. Boosting grain dry matter (DM) partitioning will

19 require increased allocation of assimilates to sink organs to enhance spike growth. A

20 high biomass spring wheat panel of 150 genotypes encompassing elite, landrace-

21 derived and synthetic-derived lines was grown under yield potential conditions in two

22 seasons in NW Mexico. Results showed that the incorporation of landrace-derived and

23 synthetic-derived backgrounds into elite lines resulted in higher expression of above-

24 ground biomass (AGDM), leaf lamina and stem DM partitioning at anthesis. However,

25 no grain yield advantage was observed over elite lines, due to lower grain number per

26 unit area (GN) and decreased harvest index (HI). Positive linear associations were

27 found among spike fertility-related traits - fruiting efficiency (grains per unit of spike

28 DM at anthesis; FE), GN and HI - which were, in turn, related positively with grain yield

29 (GY). Stem-internode 3 length and internode 3 DM partioning were negatively

30 associated with spike partitioning index (SPI: ratio of spike DM to total above-ground

31 DM at anthesis) and GN, suggesting an enhanced competition for assimilates between

32 the spike and stem internode 3 during stem elongation. Within-spike DM partitioning

33 analysis (glume, lemma, palea, rachis, awn) showed decreased partitioning to awns

34 was associated with increased FE and thousand grain weight (TGW). While the use

35 of exotic material can enhance biomass, special attention needs to be paid in the

36 selection for novel DM partitioning traits that maximize HI and GN coming from the

37 elite genepool. The selection for grain partitioning traits in wheat breeding combined

38 with sources expressing high biomass can potentially allow breeders to maximize

39 grain carbon assimilation that will deliver higher yields.

40

41 **Key words:** Grain number, spike fertility, fruiting efficiency, harvest index, wheat,

42 physiological breeding.

43 **Abbreviations:** GS: growth stage; GS65+7d/A+7d: Seven days after anthesis;

44 GS87/PM: Physiological maturity; AGDM: Above-Ground Dry Matter; DM: Dry Matter;

45 DW: Dry Weight; FW: Fresh Weight; SPI: Spike Partitioning Index; StePI: Stem

46 Partitioning Index; FE: Fruiting Efficiency; HI: Harvest Index; Ped: Peduncle; Int2:

47 Internode 2; Int3: Internode 3; Int4+: Internode 4 and below; LS: Leaf-Sheath; TS:

48 True-Stem.

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the three most important cereal crops globally and is grown on more than 214 million ha of land with an average grain yield of 3.42 t ha^{-1} (FAOSTAT, 2018). In order to meet the increasing wheat demand and maintain food security, yields must be doubled in the next 30 years (FAO, 2015; Fischer, 2014). To exploit future genetic gains in radiation-use efficiency (above-ground biomass per unit intercepted radiation) and biomass for yield potential, it will be necessary to identify diverse genetic backgrounds and traits enabling breeders to select for increased grain partitioning (Rivera-Amado et al., 2019).

During the Green Revolution, step increases in grains per m^2 (GN) and harvest index (grain dry-matter/above-ground dry matter; HI) were achieved with the introduction of semi-dwarf *Rht* genes (Fischer et al., 2014; Youssefian et al., 1992). Subsequently, wheat productivity gains have continued but at a slower rate in the last 30 to 40 years (Aisawi et al., 2015; Lopes et al., 2015) and in some regions progress has become stagnant (Brisson et al., 2010; Ray et al., 2012). Therefore, new sources of high expression of yield potential traits from diverse genetic backgrounds are required for breeders to deploy. The exploitation of the largely untapped sources of genetic diversity coming from exotic sources (wheat landraces and synthetics) has been practiced in wheat pre-breeding programs with successful results (Warburton et al., 2006; Zhang et al., 2017). Wheat landrace genotypes can also provide sources of increased biomass and thousand grain weight (TGW) (Molero et al., 2019), especially under low potential growing conditions (Lopes et al., 2015; Jaradat, 2011). Wheat synthetic genotypes (cultivars derived from *Triticum turgidum ssp. durum* × *Aegilops tauschi* crosses) have contributed higher spike population density, spike size and TGW as well as to increased resistance to diseases and abiotic stress (Breseghello & Sorrells, 2006; Li et al., 2014; Moore, 2015) and higher leaf photosynthetic rate (DelBlanco et al., 2000). Moreover, the incorporation of different genetic backgrounds into modern cultivars provides increased allelic variation of genes (Rebetzke et al., 2018) which has gradually been lost through domestication (Ozdemir et al., 2015) underpinning wheat improvement in spike fertility, GN, HI and grain yield (Ehdaie et al., 2006, Furbank et al., 2015, Hedden, 2003).

Grain yield is determined by the above-ground dry matter per unit area (AGDM) (Giunta et al., 2009) and the harvest Index (Slafer et al., 1990). Harvest index has a hypothetical limit of *ca*. 0.65 in wheat (Austin, 1980; Foulkes et al., 2011). In the last

83 decades, there has been little significant progress in its maximum expression since
84 post-Green Revolution values of ca. 0.45-0.50 in spring wheat and 0.50-0.55 in winter
85 wheat (Aisawi et al., 2015; Foulkes et al., 2011). Indeed, recent grain yield
86 improvement of CIMMYT spring wheat in the Yaqui Valley (North-West Mexico) has
87 been associated with increased biomass (Reynolds et al., 2017) but decreased HI
88 (Aisawi et al., 2015). Similar trends have been observed for genetic gains in biomass
89 in the absence of gains in HI in modern wheat cultivars under high yield potential
90 conditions in other regions (Shearman et al., 2005; Ferrante et al., 2017; Lo Valvo et
91 al., 2017), and most evidence indicates that grain growth is currently mainly sink-
92 limited under optimal conditions (Alonso et al., 2018). Therefore, strategies to improve
93 GN and HI represent important avenues for genetic gains in yield potential (Beche et
94 al., 2014; Foulkes et al., 2011; Reynolds et al., 2012).

95   One avenue to increase grains per m^2 and HI is to optimize the distribution of
96 assimilates among the plant organs at anthesis to favour spike growth whilst
97 maintaining photosynthetic capacity (Foulkes et al., 2011). In a field study on 26
98 CIMMYT elite spring wheat lines (CIMCOG panel), Rivera-Amado et al. (2019)
99 reported stem partitioning index (ratio of stem DM to above-ground DM; StePI) at
100 seven days after anthesis (GS65+7d) ranged from 0.32 to 0.41, spike PI (SPI) from
101 0.21 to 0.26, leaf-lamina PI (LamPI) from 0.18 to 0.23 and leaf-sheath PI (LSPI) from
102 0.16 to 0.20. These results indicated raising SPI offers scope for increasing grains per
103 m^2 (Gaju et al., 2009; 2014). Moreover, the fruiting efficiency (grains per unit spike DM
104 at anthesis; FE) has the potential to be additive to SPI (Foulkes et al., 2011; Lázaro &
105 Abbate, 2012; Slafer et al., 2015). There is clear variability in SPI and FE among
106 modern spring wheat cultivars and recent work has demonstrated that, although there
107 is often a trade-off between SPI and FE, high SPI and high FE may be combined in
108 some genotypes (Alonso et al., 2018; González, et al., 2011; Gonzalez-Navarro et al.,
109 2015). Rivera-Amado et al. (2019) reported increased SPI was correlated with reduced
110 StePI and reduced partitioning to stem internode 2 (top down, internode below
111 peduncle) and 3 was most effective in increasing spike SPI and spike DM per unit area
112 at anthesis +7d. Shorter internode 3 was associated with increased SPI and spike DM
113 per unit area; no association with the peduncle DM partitioning was observed.
114 Avenues to increase FE may include optimizing dry-matter partitioning within the spike
115 structural components: awn, lemma, glume, palea or rachis (Abbate et al., 1998;
116 Foulkes et al., 2011; Slafer et al., 2015). For example, Rivera-Amado et al. (2019)

117 reported a positive association between FE and lemma DM partitioning and a negative
118 association between the FE and rachis DM partitioning (as a proportion of non-grain
119 spike DM at GS65+7d) in the CIMCOG spring wheat panel. There is a need to quantify
120 the effects of these grain-partitioning traits in high biomass backgrounds and in diverse
121 genetic backgrounds relating to synthetic-derived and landrace-derived germplasm.

122   The aim of this study was to identify grain dry-matter partitioning traits to increase
123 grain number, HI and grain yield in a high biomass spring wheat association panel
124 (HIBAP) including genotypes with exotic background. Field experiments were carried
125 out over two seasons in NW Mexico under fully irrigated conditions to evaluate
126 biomass production and DM partitioning traits. Specific objectives were to: (i) quantify
127 effects of incorporation of landrace and synthetic pedigrees on expression of yield-
128 related traits, (ii) identify stem-internode traits determining genetic variation in spike
129 partitioning index and HI and (iii) identify spike structural partitioning traits (awn,
130 lemma, glume, palea or rachis) determining genetic variation in fruiting efficiency and
131 HI.
132
133 **2. Materials and Methods**

134 *2.1 Plant material and experimental design*

135   A CIMMYT spring bread wheat High Biomass Association Panel (HiBAP) of 150
136 genotypes, comprising four genotype groups (landrace-derivatives (11), synthetic-
137 derivatives (26), synthetic-and-landrace-derivatives (14) and elite cultivars (99); Table
138 S1) was grown at the Norman E. Borlaug experimental station near Ciudad Obregon,
139 Sonora, Mexico (27°N, 110°W and 38 m above the sea level) in two seasons (Y16:
140 2015-16 and Y17: 2016-17). Experiments were sown using an alpha-lattice design
141 with four replicates in raised beds (2 beds per plot, each 0.8 m x 4 m) with four (Y16)
142 and two (Y17) rows per bed (0.1 m and 0.24 m between rows, respectively) with a
143 seed rate of 102 kg ha^{-1}.

144   Irrigation was supplied using a gravity-based system with the first application either
145 shortly after (Y16) or before (Y17) sowing and then every 3 to 4 weeks. Herbicides
146 (Buctril: Bayer AG and Starane: Dow AgroSciences LLC) for broad-leaved weeds,
147 fungicide (Folicur: Bayer AG) and insecticide (Muralla: Bayer AG) were applied as
148 required to minimize the effects of weeds, diseases and pests. An application of
149 fertilizer nitrogen (50 kg N ha^{-1}) as urea was applied during land preparation, followed
150 by an application of triple super phosphate (50 kg P ha^{-1}) at sowing. A second and

151 third N application (50, 150 kg N ha^{-1} respectively) as urea was applied at the same

152 time as the first and second irrigations, respectively. The experiments were sown on

153 23 November 2015 and 23 November 2016 with date of 50% emergence on 7

154 December 2015 and 30 November 2016, respectively. Metereological data were

155 collected at an automated meterological station located within 1 km of the field

156 experiments (Table S2).

157

158 *2.1 Crop measurements*

159 *2.1.1. Development, biomass and dry matter partitioning at GS65+7d*

160 Development stages were recorded at anthesis (GS65) and at physiological

161 maturity (PM, 50% of shoots with yellow-green peduncle, GS87) (Zadoks *et al*., 1974).

162 The stages were recorded when 50% of the fertile shoots in the plot had reached the

163 specific stage (Pask et al., 2012). At GS65+7d, plants were sampled by cutting at

164 ground level in a 0.8 x 0.5 m quadrat (at least 50 cm from ends of plots) in two

165 replicates. A sub-sample consisting of 100 shoots was taken and the weight recorded

166 before and after oven drying at 70°C for 48 h to constant weight to calculate

167 aboveground dry matter at this stage (AGDM$_{A7}$). Before oven drying, infertile shoots

168 (those without an emerged spike) were counted in the sub-sample; the remaining

169 shoots were classified as fertile. From the remaining sample, 12 randomly selected

170 fertile shoots were separated into: i) leaf lamina ii) leaf sheath and stem and iii) spike.

171 The weight of each plant component was recorded after drying at 70°C for 48 h to

172 constant weight. The DM partitioning indices of each component were calculated as

173 the ratio of plant component DM to the aboveground DM. In addition, the lengths of

174 stem internodes: i) peduncle, ii) internode 2 (internode below peduncle) and iii)

175 internode 3 were measured with a ruler.

176 For a subset of 29 genotypes (subset 1), selected to be representative of genetic

177 variation in DM partitioning in the panel (see Table S1 for genotype names), stems of

178 the 12 shoots were further separated into true-stem (TS) and leaf sheath (LS) for each

179 of the peduncle (Ped), internode 2 (Int2) and internode 3 (Int3); and the internode 4

180 and below (TS+LS) (Int4+). The dry weights were recorded for each component after

181 oven drying at 70°C for 48 h. Finally, for a second subset (subset 2) comprising 14 of

182 the 29 genotypes used in subset 1 (see Table S1 for genotypes names), the 12 spikes

183 were further dissected into: i) glume, ii) lemma, iii) palea, iv) rachis and v) awn. The

184 components were bulked for the 12 spikes and weighed separately after drying at 70°C
185 for 48 h.
186
187 *2.1.2 Plant height and spike and awn length*
188 Plant height and spike and awn length were measured in two replicates on five shoots
189 per plot shortly before physiological maturity. Height was measured from the soil
190 surface to the tip of the spike (excluding awns), spike length from the spike collar to
191 the tip of the terminal spikelet (awns were excluded) and awn length from the tip of the
192 terminal spikelet to the tip of the longest awn.
193
194 *2.1.3 Grain yield and yield components*
195 At physiological maturity (PM), 50 randomly selected fertile shoots were cut at ground
196 level in two replicates. The spikes were separated from the straw. Dry weight for spikes
197 and straw was recorded separately after drying for 48 h at 70°C. The spikes were
198 threshed and the grain dry weight recorded after drying for 48 h at 70°C. Grain yield
199 was machine-harvested (expressed as 100% DM) in a plot area of 3 to 4 m^{-2},.
200 Thousand grain weight (TGW) was calculated after drying a grain sample for 48 h at
201 70°C using the image analysis system SeedCounter (SeedCountSC5000 Image
202 Analyser). From the data, spikes m^{-2} (SM2), grains m^{-2} (GN), HI, final AGDM per unit
203 area and fruiting efficiency (FE; grains per unit spike DM at seven days after anthesis)
204 were calculated.
205
206 *2.1.4. Stem water soluble carbohydrate utilization*
207 The percentage water soluble carbohydrate (WSC) of the stem was assessed using
208 the anthrone method. Chemical analyses (anthrone method; van Herwaarden et al.,
209 1998) was used to quantify % WSC content of stem and leaf sheath samples. The
210 concentration of WSC is expressed as a percentage (%WSC) on a 100% DM basis.
211 The WSC utilized for grain filling was calculated as the difference in WSC% from
212 GS61+7d to physiological maturity.
213
214
215 *2.2. Statistical analysis*
216   Significant variation for traits amongst the four genetic groups in the HiBAP
217 (landrace-derived, synthetic-derived, landrace+synthetic-derived and elite lines) was

218 tested for using the T-test procedure. Analysis of variance for phenotypic data was
219 carried out using the Multi Environment Trail Analysis R interface (META-R) for
220 Windows (Alvarado et al., 2018; Vargas et al., 2013). For each trait and genotype,
221 BLUEs (best linear unbiased estimators) were estimated, considering genotype as a
222 fixed effect and replicate as a random effect. Combined analysis of variance across
223 years was done considering genotypes and years as random effects. A covariate for
224 anthesis date as a fixed effect was included in the analyses of variance when this had
225 a significant effect ($P<0.05$), excluding phenological or dependent traits.

226   GenStat 17th edition (VSN International) was used for calculating the Pearson's
227 correlation coefficients, linear/non-linear regressions between traits and for stepwise
228 multiple linear regression analysis using the BLUEs obtained with META-R. For
229 stepwise regression analysis, the variable selected to be explained was dependent
230 and those variables tested acted as independent variables.

231

232 **3. Results**

233   Considering their breeding history and pedigree, the 150 HiBAP wheat genotypes
234 were divided into four groups (Table S1): 99 elite genotypes (i.e. progeny of crosses
235 between elite×elite), 11 landrace-derived genotypes, 26 synthetic- derived genotypes,
236 and 14 genotypes with a synthetic+landrace (s+l) pedigree (Molero et al., 2019).
237 Genetic variation in the traits measured at GS65+7d and physiological maturity is
238 described for the complete panel and for the four pedigree groups (Table 1).

239

240 *3.1 Grain yield and yield components at physiological maturity*

241   Averaging over seasons, grain yield ranged amongst the HiBAP lines from 485-
242 705 g m^{-2} ($P<0.001$; Table 1). Genetic variation was significant for most traits, including
243 above-ground DM at physiological maturity (AGDM$_{PM}$) which ranged from 1105-1642
244 g m^{-2} ($P<0.001$) and HI from 0.40-0.53 ($P<0.001$). Grain yield, AGDM$_{PM}$, HI and all
245 yield components, except spikes m^{-2}, showed significant genotype (G) x year (Y)
246 interaction and high heritabilities were obtained for most of these traits ($H^2>0.7-0.5$;
247 Table 1).

248   Among the different pedigree groups, there was no significant difference in grain
249 yield. The elite group had higher HI (0.47) compared to the synthetic-derived (0.46),
250 synthetic+landrace-derived (0.46) and landrace-derived groups (0.45). Elite lines,
251 however, accumulated less AGDM$_{PM}$ (1,346 g m^{-2}) than the other three groups (1,358-

252   1,394 g m^{-2}) as observed by Molero et al. (2019). Elite lines also had higher GN but

253   lower TGW than the other three groups. Positive linear relationships were observed

254   amongst genotypes between grain yield and AGDM$_{PM}$ (*P<0.001*; Fig. 1a), HI (*P<0.001*;

255   Fig. 1b) and GN (*P<0.001*; Fig. 1c). A strong negative association was observed

256   between GN and TGW (*P<0.001*; Fig. 1d) and between AGDM$_{PM}$ and HI (*P<0.001*;

257   Fig. 1e).

Table 1. Means of traits at anthesis (GS65) + 7 days and physiological maturity (GS87) for elite (99 lines), landrace-derived (LD: 11 lines), synthetic- derived (SD: 26 lines) and synthetic+landrace-derived (S+LD: 14 lines) groups and phenotypic ranges, least significant differences (LSD: *p=0.05*), significance (*p-values*) and broad-sense heritability for 150 HiBAP genotypes. Values represent means of Y16 and Y17.

	Traits	Units	Elite		LD		SD		S+LD		H^2	Min	Mean	Max	LSD	P(G)	P(Y)	P(G×Y)
GS65+7d anthesis	DTA	Days	76	B	79	A	76	B	76	B	0.87	68	76	85	3.01	***	***	***
	$AGDM_{A+7}$ [†]	g m⁻²	856	B	891	A	867	AB	872	AB	0.60	701	861	1005	129.9	***	***	*
	LamPI		0.21	B	0.22	A	0.21	B	0.21	B	0.68	0.17	0.21	0.26	0.03	***	**	ns
	SPI [†]		0.27	A	0.26	B	0.26	B	0.27	A	0.75	0.21	0.27	0.32	0.03	***	ns	*
	StePI		0.52	B	0.52	B	0.53	A	0.52	B	0.76	0.46	0.52	0.57	0.03	***	*	***
	FE [†]	grains g⁻¹	51.5	A	46.0	B	49.0	A	44.5	B	0.73	41.5	58.7	84.2	14.0	***	ns	*
	$DMSpk_{A+7}$	g m⁻²	258.4	A	259.8	A	254.9	A	251.7	A	0.48	171.4	240.1	320.7	57.8	**	ns	ns
GS87	DTM	Days	115	B	117	A	114	C	114	C	0.85	105	115	124	3.35	***	***	***
	$AGDM_{PM}$	g m⁻²	1346	B	1394	A	1358	AB	1389	A	0.51	1105	1355	1642	206.3	***	**	***
	GY	g m⁻²	597	A	592	A	594	A	593	A	0.60	485	596	705	71.5	***	ns	***
	TGW	G	42.6	C	45.7	B	45.6	B	48.2	A	0.94	30.0	43.9	53.8	2.92	***	***	***
	HI		0.47	A	0.45	C	0.46	B	0.46	B	0.80	0.40	0.47	0.53	0.04	***	ns	*
	GN	grains m⁻²	14077	A	13118	B	13096	B	12320	C	0.83	10382	13643	16669	16727	*	ns	***
	SM2	spikes m⁻²	307.6	A	287.7	B	301.5	A	283.5	B	0.86	234	303	411	46.5	***	**	ns

DTA: Days from emergence to seven days after anthesis; **AGDM:** Above-ground DM; **LamPI:** Lamina Partitioning Index; **SPI:** Spike Partitioning Index; **StePI:** Stem Partitioning Index; **DMSpk:** DM Spike per unit area; **DTM:** Days from emergence to physiological maturity; **FE:** Fruiting Efficiency; **GY:** Grain Yield; **TGW:** Thousand Grain Weight; **HI:** Harvest Index; **GN:** Grain Number; **SM2:** Spikes per unit area.

P(G): Significance of the genotype; *P(Y):* Significance of the year; *P(G×Y):* Significance of the genotype x environment; **H²:** Broad sense heritability (cross-year analysis).

*P<0.05; **P<0.01; ***P<0.001; ns = non-significant.

† adjusted means using DTA as covariate.

Means followed by the same letter are not significantly different (*P<0.05*) according to pairwise t tests.
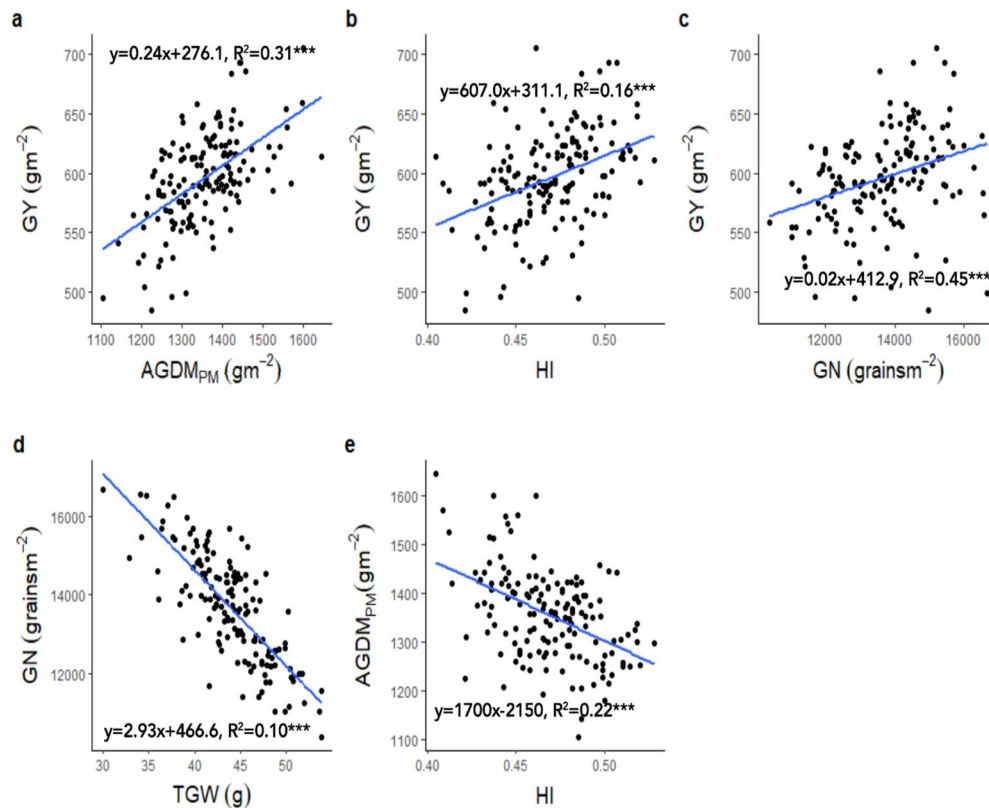
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Figure 1. Linear regressions between grain yield (GY) at 100% DM and above-ground dry matter at physiological maturity (AGDMPM), harvest index (HI) and yield components amongst the 150 HIBAP genotypes: Values presented are cross-year means (Y16 and Y17)

3.2. Biomass, DM partitioning and stem-internode lengths at GS65+7d

Averaging over years, above-ground DM at anthesis (GS65) + 7 days ($AGDM_{A+7}$) ranged amongst genotypes from 701-1,005 g m^{-2} ($P<0.001$) showing G×Y interaction ($P<0.05$; Table 1). The stem (true stem+leaf sheath) accounted for the highest proportion of $AGDM_{A+7}$ ranging from 0.46-0.57 ($P<0.001$); then the spike from 0.21-0.32 ($P<0.001$) and the leaf lamina from 0.17-0.26 ($P<0.001$; Table 1). Landrace-derived lines accumulated more $AGDM_{A+7}$ (891 g m^{-2}) than the elite lines (856 g m^{-2}), and also had higher LamPI and later DTA (3 days) than the other pedigree groups. In contrast, elite lines had higher spike partitioning index (spike DM / above-ground DM, at GS65+7d; SPI) (0.27) compared with landraces-derived and synthetic-derived lines (0.26). The synthetic-derived group was characterized by higher StePI (0.53)

271 compared to the elite, synthetic landrace and synthetic+landrace groups (0.52).

272 Fruiting efficiency was higher in the elite group (51.5 grains g^{-1}) than the landrace-

273 derived (46.0 grains g^{-1}) or the synthetic+landrace group (44.5 grains g^{-1}) ($P< 0.05$;

274 Table 1).

275   Plant height ranged amongst the 150 HIBAP lines from 84.6-114.0 cm ($P< 0.001$;

276 Fig. 2). The peduncle was the longest stem internode (genetic range 29.0-42.8 cm),

277 followed by internode 2 (LInt2; 14.2-23.6 cm) and internode 3 (LInt3; 9.9-16.7 cm) (Fig.
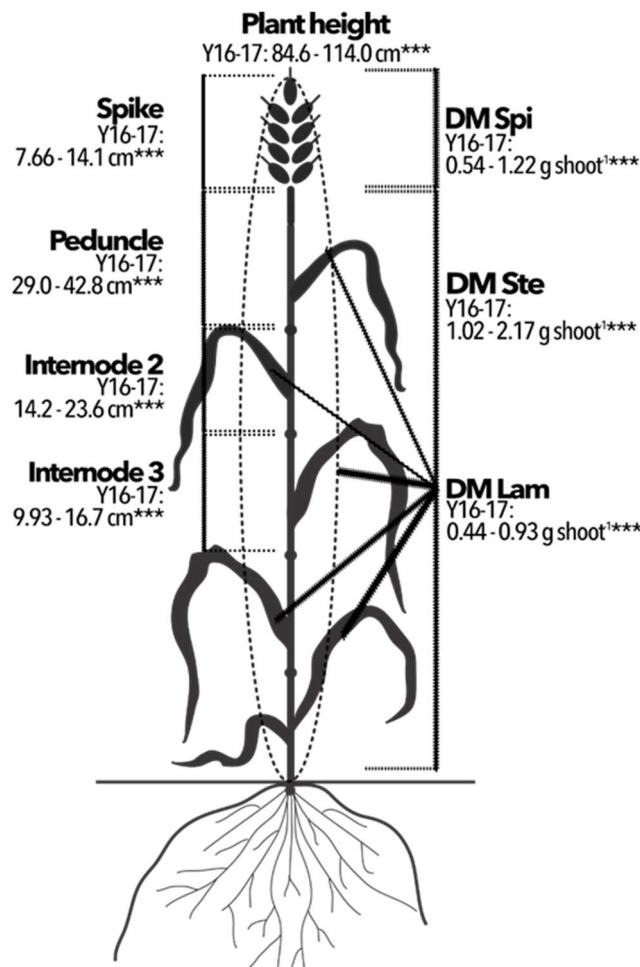
278 2).

Figure 2. Genetic ranges for 150 HiBAP genotypes for DM shoot^{-1} at GS65+7d (right) in spike (Spi), lamina (Lam) and stem (Ste) and spike and stem-internode lengths (left).
*P<0.05; **P<0.01; ***P<0.001; ns: non-significant*
Values presented are cross-year means (Y16 and Y17).

279   Among the four pedigree groups landrace-derived lines (103.3 cm) were taller than

280   the elite cultivars (98.5 cm). Peduncle length of the landrace-derived (39.3 cm) and

281   synthetic+landrace-derived groups (39.0 cm) was greater compared to the synthetic-

282   derived (38.0 cm) and elite groups (36.9 cm). The synthetic-derived (19.5 cm), elite

283   (19.3 cm) and synthetic +landrace-derived (19.4 cm) groups had slightly greater stem

284   internode 2 length than the landrace-derived group (19.0 cm) (Table 2). The four

285   groups only differed slightly for stem internode 3 length in the range 13.6-14.1 cm.

286

Table 2. Cross-year (Y16 and Y17) means for the four pedigree groups of the HiBAP for plant height (PH), spike length (LnSpk), awn length (LnAwn), peduncle length (LnPed), stem internode 2 length (LnInt2) and internode 3 length (LnInt3).

Trait	Units	Elite		Landrace		Synthetic		Synthetic+ landrace	
PH		98.5	D	103.3	A	100.5	C	101.7	B
LnSpk		12.0	C	12.8	A	11.5	D	12.3	B
LnAwn	cm	6.34	B	6.72	A	6.22	B	6.27	B
LnPed		36.9	C	39.3	A	38.0	B	39.0	A
LnInt2		19.4	A	19.0	B	19.5	A	19.3	AB
LnInt3		13.6	C	14.0	AB	13.8	BC	14.1	A

Means followed by the same letter are not significantly different ($P<0.05$) according to pairwise t tests.

287

288   The lengths of the stem peduncle (ped), internode 2 (int2) and internode 3 (int3)

289   were negatively associated with SPI ($P< 0.01$; Fig. 3a), with the strongest association

290   with int3 ($P< 0.05$). As expected stem-internode lengths were positively associated

291   with stem partitioning index (StePI; Fig. 3b). For lamina partitioning index (LamPI), a

292   negative association was observed with int2 length ($P< 0.01$), but there was no

293   signficant association with the length of the other two internodes (Fig. 3c). There was

294   a negative association between int2 length and spike DM per unit area (DMSpk$_{A+7}$)

295   ($P< 0.01$), but no signficant association was found with ped and int3 length (Fig. 3d).
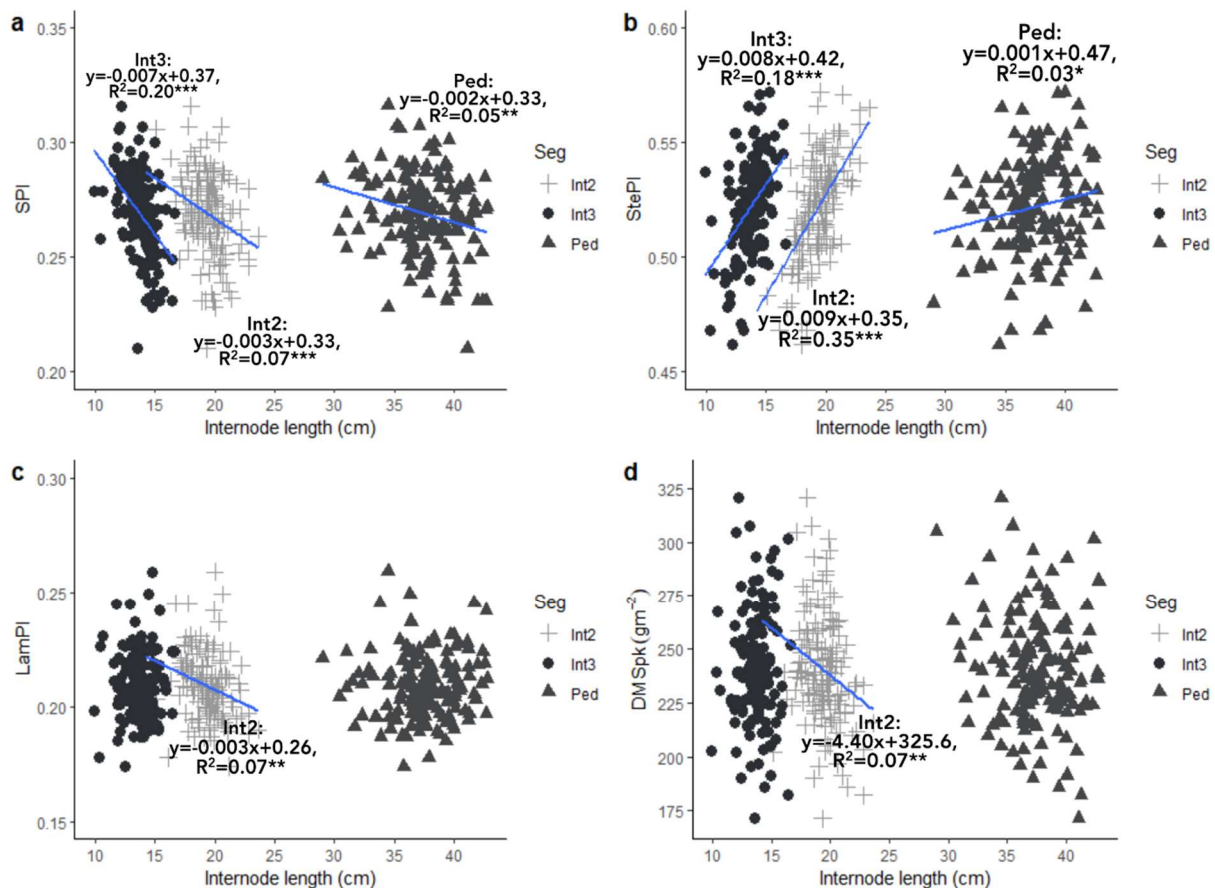
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Figure 3. Linear regressions amongst 150 HiBAP genotypes between stem internodes lengths (ped: peduncle, int2: internode 2 and int3: internode 3) and a) spike partitioning index (SPI), b) stem partitioning index (StePI), c) lamina partitioning index (LamPI) and d) spike DM per m^2 at GS65+7d (DMSpk).

3.3 Correlations between DM partitioning traits, grain number, harvest index and yield

A strong negative linear relationship was found among the 150 genotypes between stem partitioning index and spike partitioning index ($P<0.001$) and spike DM per unit area (DMSpk$_{A+7}$) ($P<0.001$). Spike partitioning index was positively associated with HI ($P<0.01$) and GN ($P<0.001$), but was negatively associated with grain yield. The latter effect may have partly related to the strong trade-off between HI and above-ground biomass at physiological maturity ($P<0.001$) in the HIBAP genotypes. Fruiting efficiency (grain number per unit non-grain spike DM at GS65+7days) was positively related with GN ($P< 0.001$), HI ($P< 0.001$) and GY ($P<0.05$). The FE showed a strong negative association with DMSpk$_{A+7}$ ($P<0.001$). There were also trade-offs between GN and thousand grain weight (TGW: $P<0.001$) and FE and TGW ($P<0.001$; Table 3).

Table 3. Pearson's phenotypic correlation coefficients between traits measured at seven days after anthesis and physiological maturity among 150 HiBAP genotypes. Values based on means of Y16 and Y17.

	GN	HI	TGW	GY	AGDM$_{PM}$	SPI	StePI	FE	PH	AGDM$_{A+7}$	LamPI	DMSpk$_{A+7}$	LInt2	LInt3	LPed
GN	-														
HI	**0.27*****	-													
TGW	**-0.76*****	-0.05	-												
GY	**0.39*****	**0.37*****	**0.28*****	-											
AGDM$_{PM}$	-0.01	**-0.50*****	**0.34*****	**0.47*****	-										
SPI	**0.23****	**0.21****	**-0.38*****	**-0.20***	**-0.34*****	-									
StePI	**-0.21****	-0.02	**0.37*****	**0.21****	**0.24*****	**-0.77*****	-								
FE	**0.65*****	**0.29*****	**-0.40*****	**0.39*****	-0.02	**-0.25*****	**0.20****	-							
PH	**-0.48*****	**-0.40*****	**0.51*****	0.00	**0.40*****	**-0.54*****	**0.46***	**-0.27*****	-						
AGDM$_{A+7}$	0.08	**-0.26*****	-0.04	0.06	**0.27*****	-0.11	0.00	**-0.48*****	**0.20****	-					
LamPI	0.00	**-0.26*****	-0.03	-0.04	0.11	**-0.24*****	**-0.43*****	0.06	0.06	**0.17***	-				
DMSpk$_{A+7}$	0.12	-0.12	**-0.14†**	-0.03	0.10	**0.44*****	**-0.41*****	**-0.43*****	-0.07	**0.52*****	0.00	-			
LInt2	**-0.27*****	**0.18***	**0.33*****	0.09	-0.06	**-0.50*****	**0.62*****	-0.01	**0.36*****	0.07	**-0.24*****	**-0.24*****	-		
LInt3	**-0.36*****	**-0.23****	**0.33*****	-0.08	**0.17***	**-0.49*****	**0.43*****	**-0.23*****	**0.63*****	**0.28*****	0.04	0.04	**0.51*****	-	
LPed	**-0.44*****	**-0.28*****	**0.39*****	-0.09	**0.21****	**-0.23*****	**0.18***	**-0.24*****	**0.60*****	-0.04	0.05	**-0.15†**	0.01	0.05	-

A+7: Anthesis + 7 days; PM: Physiological Maturity; GN: Grain Number; HI: Harvest Index; TGW: Thousand Grain Weight; GY: Grain Yield; AGDM: Above-Ground Dry Matter; SPI: Spike Partitioning Index; StePI: Stem Partitioning Index; FE: Fruiting Efficiency; PH: Plant Height; LamPI: Lamina Paritioning Index; DMSpk: Dry Matter Spikes per unit area; LInt2: Length internode 2; LInt3: Length internode 3; LPed: Length peduncle
†P<0.10; *P<0.05; **P<0.01; ***P<0.001.

3.4. Internode DM partitioning at GS65+7d

Genetic variation was measured for stem-internode DM partitioning traits at GS65+7d in the subset of 29 genotypes. The true-stem (TS) overall accumulated more DM than the leaf sheath (LS) (0.87 vs 0.45 g shoot^{-1}, for ped, int2 and int3 combined); and upper internodes accumulated progressively more DM than lower internodes (Table 4). Peduncle TSPI ranged amongst genotypes from 0.06 to 0.15, int2 TSPI from 0.05 to 0.12 and int3 TSPI from 0.05 to 0.09 (*P<0.001*). The product of internode length and TS specific weight (TS DM per unit internode length; TSSW, g cm^{-1}) determines the dry matter per TS internode; true-stem SW was progressively decreased in upper compared to lower internodes (Table 4). Genetic variation in TSSW was found for each internode (*P<0.001*); e.g. for ped TSSW 5-9 mg cm^{-1} and int3 TSSW 11-17 mg cm^{-1}.

Table 4. Genetic ranges (Min: Minimum, Mean, Max: Maximum), broad-sense heritability (H^2), and P values for genotype (G), year (Y) and genotype x year (GxY) for subset of 29 HiBAP genotypes for true-stem (TS) and leaf-sheath (LS) DM partitioning indices (PI) and specific weights (SW) at GS65+7d. Values represent means of Y16 and Y17.
Ped: Peduncle; Int2: Internode 2; Int3: Internode 3; Int4+: Internode 4+ (TS+LSPI);
*P<0.05; **P<0.01; ***P<0.001; ns: non-significant

Traits	Units	H^2	Min	Mean	Max	P(G)	P(Y)	P(G×Y)
PedTSPI		0.70	0.094	0.115	0.153	***	**	*
Int2TSPI		0.77	0.069	0.089	0.116	***	ns	ns
Int3TSPI		0.70	0.060	0.071	0.085	***	**	*
PedLSPI		0.65	0.059	0.077	0.101	***	ns	ns
Int2LSPI		0.18	0.032	0.041	0.049	ns	ns	ns
Int3LSPI		0.25	0.018	0.026	0.037	ns	ns	*
Int4+		0.79	0.045	0.087	0.117	***	*	ns
PedTSSW		0.64	0.006	0.009	0.013	***	*	ns
Int2TSSW	g cm^{-1}	0.81	0.009	0.014	0.20	***	*	ns
Int3TSSW		0.83	0.011	0.017	0.023	***	ns	ns

The correlations between stem-internode traits, grain yield, yield components, harvest index and spike partitioning traits are shown in Table 5. Spike partitioning index showed a negative association with int2 true-stem PI and int4+ PI (*P<0.05*) and with the leaf-sheath PI of each internode (*P<0.05*). Spike DM per m^2 was also negatively associated with leaf sheath PI for all the internodes, most strongly for the upper internodes (ped < int2 < int3; *P<0.10*). Negative associations were found

between each of int3 true-stem PI ($P<0.05$) and int4 (true-stem + leaf sheath) PI and grains m^{-2} ($P<0.05$). Int3 true-stem PI ($P<0.001$) and int4 (true-stem + leaf sheath) PI were also negatively associated with HI, but there was a positive association between each of ped leaf-sheath PI ($P<0.01$) and int2 true-stem PI ($P<0.10$) and HI. Spikes per m^2 showed a positive association with ped true-stem PI ($P<0.01$) and int2 true-stem PI ($P<0.10$) but a negative association with int4 (true-stem + leaf sheath) PI ($P<0.001$). In additon, ped true-stem PI showed a positive association with grains m^{-2} and grain yield ($P<0.05$ and $P< 0.001$, respectively).

Table 5. Pearson's correlation coefficient among traits measured at seven days after anthesis (SPI, DMSpk$_{A+7}$, WSC$_{Ut}$) and physiological maturity (HI, GY, GN, SM2, FE) for 29 genotypes (subset 1) of the HiBAP. Values represent means of Y16 and Y17.

Trait	Correlation coefficient (r)							
	SPI	**HI**	**GY**	**GN**	**DMSpk$_{A+7}$**	**SM2**	**FE**	**WSC$_{Ut}$**
PedTSPI	**0.25†**	**0.29†**	0.09	**0.36***	-0.16	**0.59*****	0.25	-0.09
Int2TSPI	-0.10	**0.54*****	**0.28†**	0.01	-0.13	0.13	0.08	**0.39***
Int3TSPI	**-0.55*****	0.15	0.15	**-0.41****	-0.06	**-0.45****	-0.07	0.13
PedLSPI	**-0.40***	**-0.37***	0.04	0.00	**-0.43***	0.06	**0.43***	**-0.37***
Int2LSPI	**-0.39***	-0.06	0.18	**-0.31†**	**-0.38***	-0.13	0.09	0.07
Int3LSPI	**-0.61*****	0.00	0.05	**-0.27†**	**-0.30†**	**-0.30†**	**0.27†**	-0.03
Int4+PI	**-0.47****	-0.08	0.18	**-0.41****	0.15	**-0.69*****	-0.20	0.09
PedTSSW	0.17	-0.11	**0.30†**	0.07	**0.62*****	**-0.49****	**-0.28†**	0.11
Int2TSSW	0.10	-0.12	0.21	-0.26	**0.46****	**-0.67*****	**-0.45****	0.14
Int3TSSW	-0.03	-0.24	0.10	**-0.39****	**0.33†**	**-0.69*****	**-0.42***	-0.04

Ped: Peduncle; Int2: Internode 2; Int3: Internode 3; Int4+: Rest of internodes (TS+LS); TS: True stem; LS: Leaf sheath; SW: Specific weight; SPI: Spike partitioning index; HI: Harvest index; GY: Grain yield (100% DM); DMSpkA+7: Spike DM per unit area at GS65+7d; SM2: Spikes per unit area; FE: Fruiting efficiency; WSC$_{Ut}$: Stem water soluble carbohydrate utilization.

†P<0.10; *P<0.05; **P<0.01; ***P<0.001

3.5 Spike component partitioning

Spike component partitioning was assessed at GS65+7d in a subset of 14 genotypes. DM partitioning among the spike structural components decreased in the following order: lemma (Le) > awns (Aw) > glume (Glu) > rachis (Ra) > palea (Pa). Significant genetic variation was found for all spike component partitioning indices

343   (spike component DM / non-grain spike DM) with the exception of PaPI; there was a

344   G×Y effect for GluPI, LePI and RaPI (*P<0.05*) (Table 6).

345   The correlations between spike structural components and grain yield (GY), yield

346   components, harvest index (HI) and spike partitioning traits are shown in Table 7.

347   Spike partitioning index was negatively associated with Lemma PI and rachis specific

348   weight (rachis DM / rachis length; RaSW) (*P<0.10*), but positively associated with awn

349   PI (*P<0.10*). Fruiting efficiency was positively related to lemma PI (*P<0.10*) but

350   negatively with awn PI (*P<0.10*). Whereas, spike DM per unit area at GS65+7d was

351   positively associated with awn PI (*P<0.10*) but negatively with lemma PI (*P<0.05*). The

352   rachis PI was positively correlated with grain yield (*P<0.05*), whilst rachis PI (*P<0.05*)

353   and rachis SW (*P<0.01*) were positively linked with TGW. The rachis SW was also

354   negatively associated with grains m^{-2} (*P<0.05*). Awn PI was negatively associated with

355   TGW (*P<0.10*). There was no association between any of the spike structure PIs and

356   HI.

Table 6. Genetic ranges (Min: Minimum, Mean, Max: Maximum), broad-sense heritability (H2), and significance values for genotype (G), year (Y) and genotype × year (G×Y) for 14 HiBAP genotypes for spike component DM partitioning indices (PI) and rachis specific weight (SW) at GS65+7d. Values presented are cross-year means (Y16 and Y17).

Traits	*H²*	Min	Mean	Max	*P(G)*	P(Y)	*P(G×Y)*
GluPI	0.76	0.17	0.20	0.23	*	ns	**
PaPI	0.07	0.09	0.11	0.12	ns	ns	ns
LePI	0.91	0.26	0.29	0.31	***	*	*
AwPI	0.94	0.20	0.24	0.30	***	ns	ns
RaPI	0.95	0.13	0.15	0.18	***	ns	*
RaSW	0.71	0.008	0.010	0.011	ns	ns	ns

Glu: Gluma; Le: Lemma; Pa: Palea; Ra: Rachis; Aw: Awns
P<0.05; ***P<0.01*; ****P<0.001*; ns = non-significant

Table 7. Pearson's correlation coefficient among traits measured at seven days after anthesis (SPI, DMSpk$_{A+7}$, FE) and physiological maturity (HI, GY, GN, SM2) for 14 genotypes (subset 2) of the HiBAP. Values presented are cross-year means (Y16 and Y17).

Traits	Correlation coefficient (r)						
	SPI	**FE**	**GN**	**HI**	**GY**	**TGW**	**DMSpk$_{A+7}$**
GluPI	**-0.50**†	0.22	-0.29	-0.05	-0.12	0.16	-0.34
PaPI	0.24	-0.04	0.02	0.15	-0.11	-0.11	-0.11
LePI	**-0.49**†	**0.41**†	-0.15	0.18	-0.17	0.03	**-0.53***
AwPI	**0.49**†	**-0.31**†	0.30	-0.18	-0.13	**-0.39**†	**0.43**†
RaPI	-0.07	-0.28	-0.14	0.20	**0.55***	**0.58***	0.10
RaSW	**-0.45**†	-0.17	**-0.40**†	0.18	0.34	**0.67****	-0.16

Glu: Glume; Pa: Palea; Le: Lemma; Aw: Awns; Ra: Rachis; PI: Partitioning Index; SPI: Spike Partitioning Index; FE: Fruiting Efficiency; GN: Grain number per unit area; HI: Harvest Index; GY: Grain Yield; TGW: Thousand Grain Weight; DMSpkA+7: Spike DM per unit area at GS65+7d.
†P<0.10; *P<0.05; **P<0.01; ***P<0.001

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3.6 Stepwise regression analysis for determinants of grain yield, HI and grain m^{-2}

The associations between GY, HI, and GN (as dependent variables) and selected physiological traits (independent variables) were tested in a stepwise linear regression analysis (Table 8) for the 150 genotypes and for the subset of 29 genotypes including stem-internode traits as dependent variables. For GY, 30.7% of the variation was accounted for by AGDM$_{PM}$ as a single trait, adding HI and FE increased the variation accounted for to 87.2%. As a single trait, plant height explained most phenotypic variation in HI (16%), the phenotypic variation accounted for increased by adding stem internode 2 length (27.5%), and then SM2, FE and SPI (42.2%). Fruiting efficiency was the most important trait explaining phenotypic variation for GN (46%), adding SPI and AGDM$_{A+7}$ to the model increased the variation accounted for to 88%.

The stepwise regression analysis was carried out for the 29 genotypes including the stem-internode traits in the selected physiologcal traits. For GY, AGDM$_{PM}$, int2TSPI and AGDM$_{A+7}$ explained 59.6% of the phenotypic variation. For HI, 30.1% of variation was explained by int2TSPI, adding other traits did not improve the model. Phenotypic variation for SPI was explained through LInt2, int2TSPI, and pedTSSW (47.1%) and for GN by SM2, pedTSSW and int3TSSW (55.1%).

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Table 8. HiBAP stepwise multiple linear regression analysis testing for grain yield (GY), harvest index (HI), spike partitioning index (SPI) and grain number (GN) as dependent variables against selected traits.

Traits	Variables selected	R	Prob	Variables tested in model
__Whole panel: 150 genotypes__				
GY	$AGDM_{PM}$	30.7	*<0.001*	$AGDM_{A+7}$, $AGDM_{PM}$,
	$AGDM_{PM}$, HI	86.0	*<0.001*	DTA, DTM,
	$AGDM_{PM}$, HI, FE	87.2	*<0.001*	$DMSpk_{A+7}$, FE, PH,
				HI, LInt2, LInt3,
				LPed, SPI, StePI,
				LamPI
HI	PH	16.0	*<0.001*	PH, LPed, LInt2,
	PH, LInt2	27.5	*<0.001*	LInt3, SM2, SPI, FE,
	PH, LInt2, SM2	33.0	*<0.001*	$AGDM_{A+7}$
	PH, LInt2, SM2, SPI	36.8	*<0.001*	
	PH, LInt2, SM2, SPI, FE	42.2	*<0.001*	
GN	FE	46.1	*<0.001*	PH, LPed, LnInt2,
	FE, SPI	62.6	*<0.001*	LInt3, SM2, SPI, FE,
	FE, SPI, $AGDM_{A+7}$	88.0	*<0.001*	$AGDM_{A+7}$
__Subset 1: 29 genotypes__				
GY	$AGDM_{PM}$	45.8	*<0.001*	Int2TSPI, Int3TSPI,
	$AGDM_{PM}$, Int2TSPI	54.7	*<0.01*	PedTSPI,
	$AGDM_{PM}$, Int2TSPI, $AGDM_{A+7}$	59.6	*<0.05*	PedTSSW,
				Int2TSSW,
				Int3TSSW, LInt2,
				LInt3, LPed,
				$AGDM_{PM}$, $AGDM_{A+7}$
HI	Int2TSPI	30.1	*<0.001*	
SPI	LInt2	11.7	*<0.001*	LPed, LInt2, LInt3,
	LInt2, Int2TSPI	39.1	*<0.001*	PedTSPI, Int2TSPI,
	LInt2, Int2TSPI, PedTSSW	47.1	*<0.01*	PedTSSW,
				Int2TSSW,
GN	SM2	30.0	*<0.001*	Int3TSSW, Int3TSPI,
	SM2, PedTSSW	53.3	*<0.01*	SM2, $AGDM_{A+7}$
	SM2, PedTSSW, Int3TSSW	55.1	*<0.05*	

R: Variation explained (%); Prob: Probability; A+7: Seven days after anthesis; PM: Physiological Maturity; DTA: Days from emergence to seven days after anthesis; AGDM: Above-ground DM; LamPI: Lamina Partitioning Index; StePI: Stem Partitioning Index; DMSpk: DM Spike per unit area; DTM: Days from emergence to physiological maturity; TGW: Thousand Grain Weight; Ped: Peduncle; Int2: Internode 2; Int3: Internode 3; TS: True-Stem; PI: Partitioning Index; SW: Specific weight.

4. Discussion

4.1 Effects of exotic backgrounds in the HiBAP

The grain yield of the elite lines with exotic background (landrace-derived, synthetic-derived and synthetic+landrace-derived) was not significantly different to the elite cultivars but they utilized different physiological routes to achieve the same yield. In general, the exotic genotypes produced more biomass at anthesis + 7 days, but a higher proportion was partitioned to the lamina (landrace derivatives) or to the stems (synthetic derivatives) than the spikes. The lower relative investment of dry matter in the spike and greater height in the exotic genotypes in part explained their reduced harvest index compared to elite genotypes. Lower fruiting efficiency observed in exotic backgrounds compared with the elite group also partly explained their lower grain number and harvest index. Therefore, the advantage of greater biomass at physiological maturity reported for the exotic backgrounds (Molero et al., 2019) was not translated into higher grain yield. To exploit the improved biomass of exotic backgrounds in pre-breeding programs, it will be important to identify native material that has shorter internode 3 to raise spike partitioning index and high expression of fruiting efficiency to enhance the harvest index and grain yield, or increase the number of backcrosses with elite lines to achieve the same without sacrificing the improved biomass.

4.2 Association between biomass, harvest index and grain yield

Previous studies in CIMMYT spring wheat have identified a trade-off between above-ground DM and harvest index in modern spring wheat cultivars (Aisawi et al., 2015, Rivera-Amado et al., 2019) suggesting that future increases in biomass will not impact greatly on yield if harvest index is not maintained or increased (Philipp et al., 2018; Hu et al., 2018; Reynolds *et al.*, 2017). This was also observed in the HiBAP in the present study, where across the 150 lines the above-ground DM at physiological maturity and harvest index were negatively correlated likely due in part to the contrasting effects of plant height on biomass and harvest index in the panel. Furthermore, the current experiments were sown in raised beds with a relatively large gap of 24 cm between the two beds per plot. In this planting system, taller genotypes may have achieved earlier canopy closure increasing light interception and biomass, thus contributing to the positive relation we observed between final plant height and biomass at GS65+7d and physiological maturity. Plant height in the HiBAP showed a

411 negative correlation with harvest index consistent with many previous observations in
412 wheat genotypes, e.g. amongst *Rht* (reduced height) near-isogenic lines (Flintham et
413 al, 1997; Addisu et al. 2010). Therefore, maintaining high biomass (which was more
414 strongly related with grain yield in the HiBAP than HI) while increasing HI is a major
415 objective for wheat breeders to raise yield potential. Avenues to achieve this may be
416 to improve simultaneously the spike partitioning index and fruiting efficiency (Rivera-
417 Amado et al., 2019); each of these traits showed a positive association with grains m-
418 2 and harvest index in the HiBAP panel.
419
420 *4.3 Avenues to increase spike partitioning index in high biomass lines*
421   Genetic differences in aboveground biomass at anthesis + 7 days were not
422 associated with GN in the HiBAP. Genetic variation in SPI was, as expected, positively
423 associated with GN and HI, consistent with floret survival being determined by
424 assimilate availability to the spike during the latter stages of stem-elongation (Slafer
425 Foulkes et al., 2011). However, there was a trade-off between biomass at anthesis +
426 7 days and SPI, likely partly mediated by contrasting effects of plant height on biomass
427 (positive association) and SPI (negative association) at this stage. Decreased plant
428 height with the semi-dwarf Rht genes decreased stem DM partitioning and increased
429 spike growth and GN since stem and spike growth overlap during the rapid spike
430 growth phase from booting to anthesis (Satorre & Slafer, 1999; Fischer & Stockman,
431 2006). Plant height at ca. 70-100 cm in modern semi-dwarf wheat cultivars may now
432 be close to optimal (Addisu et al., 2010; Slafer et al., 2015). However, further stem-
433 length reductions targeted to specific internodes with small effects on overall height
434 may be feasible to increase spike partitioning index, especially in CIMMYT spring
435 wheat cultivars where plant height is presently in the range 100 to 110 cm (Aisawi et
436 al., 2015). Nevertheless, targeted reductions in stem-internode length may need to be
437 done with caution in winter wheat in NW Europe where plant height is presently in the
438 range of 80 to 90 cm (Pask et al., 2012; AHDB, 2017) as suboptimal canopy
439 architecture and light distribution could impact radiation-use efficiency resulting in
440 decreases in biomass and/or stem water-soluble carbohydrates (Fischer, 2007;
441 Semenov et al., 2014).
442   The competition for assimilates between the spike and the stem will differ
443 depending on the stem-internode position as maximum stem-growth rates have been
444 reported to vary from 7-21 days after anthesis (Ehdaie et al., 2006). In the HiBAP

445   subset of 29 genotypes, spike partitioning index was strongly negatively associated

446   with int3 true-stem PI, but was not associated with int2 true-stem PI; SPI was positively

447   associated with ped true-stem PI. Rivera-Amado et al. (2019) reported in 26 CIMMYT

448   elite spring wheat cultivars that internode 2 and 3 true-stem PIs were negatively

449   associated with SPI and spike DM (g m^{-2}), but there was no association with ped true-

450   stem PI. In our study across all 150 genotypes, there was a stronger negative

451   correlation between stem-internode 3 length and SPI than for the peduncle length and

452   SPI, in general agreement with Rivera-Amado et al. (2019) that stem-internode 3

453   showed the strongest correlation amongst the stem internodes with spike growth. Our

454   results suggest stem internode 3 may compete more strongly with the spike for

455   assimilate than the peduncle, which may partly reflect that half of the extension for the

456   peduncle occurs after anthesis when rapid spike growth has ceased. Rivera-Amado et

457   al. (2019) found no association between spike density and stem-internode PIs, but our

458   results showed higher spike density increased DM partitioning to the ped true-stem

459   and decreased DM partitioning to internode 4 (true stem and leaf sheath). Overall,

460   shoot density at 303 m^{-2} was lower in the HiBAP than in the CIMCOG panel reported

461   on by Rivera-Amado et al. (2019) at 444 m^{-2}, and lower spike densities in the HiBAP

462   may have resulted in greater light penetration to lower stem phytomer levels favouring

463   DM growth in internode 4 relative to the peduncle, in comparison to higher spike

464   densities. This may also partly explain why SPI showed a negative association with

465   int3 true-stem PI, but a positive association with ped true-stem PI in our study.

466   Our results showed int3 true stem PI was negatively associated with GN and

467   ped true-stem PI was positively associated with GN, consistent with the effects

468   observed for these stem-internode PIs on spike partitioning. However, int3 true-stem

469   PI was not associated with HI, and int2 true-stem PI and ped true-stem PI were each

470   positively associated with HI. A positive association between int2 true-stem PI and

471   stem water soluble carbohydrate utilization may have contributed to its positive

472   association with HI; true stem PIs for other internodes were not significantly associated

473   with stem WSC utilization. Stem carbohydrate reserves may contribute from 10 to 62%

474   of the final grain weight under yield potential conditions (Ehdaie et al., 2008). In

475   addition, the positive associations between each of int2 true-stem PI and ped true-

476   stem PI and HI were likely also related with the positive association between these

477   true stem PIs and TGW. Our results indicated that maintaining plant height but

478   reducing stem int3 length and int3 true-stem partitioning relative to other TS internodes

479 could be a strategy to increase spike fertility (spike partitioning index and grain
480 number). Since the basal internodes (int4+) are the most important for plant support
481 (lodging resistance), this approach should also be consistent with maintaining lodging
482 resistance in high yield potential cultivars (Piñera-Chavez et al., 2016).

483

484 *4.4 Avenues to increase fruiting efficiency*

485   Present results showed that fruiting efficiency had a stronger positive correlation
486 with GN and HI than spike partitioning index and was also positively correlated with
487 grain yield. Other studies on spring wheat have also found a strong association
488 between FE and grain number (Bustos et al., 2013; Elía et al., 2015; Rivera-Amado et
489 al., 2019). In the subset of 14 genotypes, increased FE was associated with decreased
490 awn PI and increased lemma PI. Decreased allocation of assimilates to awns may be
491 a strategy to increase floret fertility in irrigated environments since this represents a
492 saving of spike dry matter which can be reallocated to floret growth. However, there
493 would be a loss of photosynthetic capacity associated with a reduction in awn
494 photosynthesis which potentially could affect grain growth in environments subject to
495 stress (Maydup et al., 2014) or yield potential (Sanchez-Bragado et al., 2016). The
496 mechanistic basis for the association between lemma PI and FE is not clear; it is
497 possible that this was not a causal effect but rather an indirect effect of the strong
498 negative association between awn PI and lemma PI. Rebetzke et al. (2016) also found
499 awns reduced grain number in irrigated and rainfed spring wheat in Australian.
500 Although rachis PI was not associated with FE, it showed a positive association with
501 grain weight and grain yield; it can be speculated that increased rachis PI was
502 associated with improved vascular connections within the rachis and reduced
503 resistance to assimilate supply to the distal spikelets hence increased grain weight in
504 distal spikelets (González et al., 2011). Alternatively, a longer rachis could be
505 associated with an increase in rachis length per spikelet reducing physical restrictions
506 to grain size and/or increasing spike photosynthesis (Gaju et al., 2014). The negative
507 relation between rachis specific weight and the amount of grains could potentially be
508 associated with similar mechanisms.

509   In the HIBAP lines, fruiting efficiency was negatively associated with spike DM per
510 unit area and spike partitioning index. Similar results were reported for two high FE
511 cultivars by Terrile et al. (2017) who suggested that higher values were more caused
512 by a reduction in spike DM than an increment in grain number. Gonzalez et al. (2011)

513   reported that the trade-off between FE and spike partitioning index was greatest in
514   genotypes with greater DM spike, which did not efficiently translate DM into grain
515   resulting in excessive final spike DM as chaff (González et al., 2011). Our results also
516   showed a trade-off between FE and chaff DM at harvest (data not shown). It has also
517   been suggested that the trade-off may be associated with genotypes with larger spikes
518   having a limited assimilate supply to distal florets within spikelets due to restricted
519   vascular connections within the rachilla (Slafer et al., 2015).
520
521   *4.5 Implications for breeding programs*
522   High-throughput phenotypic platforms are required to measure traits in a precise
523   and cost-effective way in breeding programmes (Summerer et al., 2019). Most of the
524   traits measured in the present experiments at anthesis + 7 days and physiological
525   maturity required sampling shoots from the field followed by destructive growth
526   analysis. This type of methodology is feasible in experiments with a moderate number
527   of genotypes (~100 to 200). However, methods used in current experiments were
528   laborious and time-consuming. To phenotype plant morphology traits (plant height and
529   peduncle, awns and spike lengths in the HiBAP panel for 150 genotypes (two
530   replicates per genotype), required around 48 person-days. The detailed stem-
531   internode and spike-morphology measurements required around 40 person-days to
532   obtain the data for 150 genotypes in two replicates. Therefore, these methodologies
533   cannot be effectively applied in wheat breeding programmes at the stage of early
534   progeny selection with many thousands of genotypes to screen. However, they could
535   be measured in parental lines with the view to strategic crossing for trait stacking since
536   more manageable numbers are involved.
537   The traits to be deployed in plant breeding should also be selected according to
538   good phenotypic plasticity and heritability (Cooper & Bänziger, 2017; Sadras &
539   Rebetzke, 2013). In this study, most of the grain partitioning traits had heritability >
540   0.50, e.g. stem-internode lengths > spike partitioning index > fruiting efficiency,
541   generally agreeing with other studies in wheat (Lopes et al., 2012; Sukumaran et al.,
542   2017). Pyramid selection of these traits could therefore help to narrow the selection of
543   parental crosses going into the breeding programme (Reynolds et al., 2017). For
544   several of the spike structural traits associated with fruiting efficiency and grain
545   number, e.g. awn PI and rachis specific weight, current phenotyping methods are time
546   consuming and no medium to high-throughput field screens are presently available. In

547 these cases, the implementation of QTLs for selection for traits can potentially
548 counteract this shortcoming of labour-intensive phenotyping. Therefore, the genetic
549 basis of these traits must be established in future studies for deployment in marker-
550 assisted selection in breeding.
551

560

561

562 **References**

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2. Supplementary material

Table S1. HiBAP genotypes names, subset and pedigree classification considering their breeding/crossing history.

	Genotype	Subset 1	Subset 2	Detail classification	General classification
1	CIRNO C 2008			Elite	Elite
2	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/7/CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO			Elite-Introgression	Elite
3	SIETE CERROS T66	✖	✖	Elite	Elite
4	PAVON F 76	✖		Elite	Elite
5	SERI M 82			Elite	Elite
6	BACANORA T 88			Elite	Elite
7	ATTILA			Elite	Elite
8	BAVIACORA M 92			Elite	Elite
9	SERI/RAYON			Elite	Elite
10	BRBT1*2/KIRITATI			Elite	Elite
11	PFAU/WEAVER*2//TRANSFER#12,P88.272.2			Elite	Elite
12	KRICHAUFF	✖	✖	Elite-Introgression	Elite
13	BECARD			Elite	Elite
14	SAUAL/WHEAR//SAUAL			Elite	Elite
15	WBLL1*2/4/BABAX/LR42//BABAX/3/BABAX/LR42//BABAX			Elite	Elite
16	KFA/3/PFAU/WEAVER//BRAMBLING/4/PFAU/WEAVER*2//BRAMBLING	✖	✖	Elite	Elite
17	KINGBIRD #1//INQALAB 91*2/TUKURU			Elite	Elite
18	UP2338*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/MILAN/KAUZ//CHIL/CHUM18/6/UP2338*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ			Elite	Elite
19	CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO			Elite-Introgression	Elite
20	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/7/CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO			Elite-Introgression	Elite
21	SOKOLL//PUB94.15.1.12/WBLL1			Syn+Lan derivated	Syn+Lan derivated
22	BCN/WBLL1//PUB94.15.1.12/WBLL1			Landrace-derivated	Landrace-derivated
23	WBLL1*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/KACHU #1			Elite	Elite
24	KRL 210	✖		Elite	Elite
25	TECUE #1/2*WAXWING			Elite	Elite
26	CHEWINK #1	✖	✖	Elite	Elite
27	PASTOR//HXL7573/2*BAU/3/WBLL1			Elite	Elite
28	CHEN/AE.SQ//WEAVER/3/SSERI1	✖	✖	Syn-derivated	Syn-derivated
29	SOKOLL/3/PASTOR//HXL7573/2*BAU/4/WBLL4//OAX93.24.35/WBLL1			Syn+Lan derivated	Syn+Lan derivated
30	SOKOLL/3/PASTOR//HXL7573/2*BAU/4/PARUS/PASTOR			Syn-derivated	Syn-derivated
31	SOKOLL/3/PASTOR//HXL7573/2*BAU/4/SOKOLL/WBLL1			Syn-derivated	Syn-derivated
32	PAVLOVKA/V15.89C//NAVJ07/3/ROLF07			Elite	Elite
33	SOKOLL/3/PASTOR//HXL7573/2*BAU/4/ATTILA/PASTOR			Syn-derivated	Syn-derivated

#	Pedigree			Class 1	Class 2
34	WBLL4//OAX93.24.35/WBLL1/5/CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2			Syn+Lan derived	Syn+Lan derived
35	SOKOLL/WBLL1			Syn-derived	Syn-derived
36	CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2			Syn-derived	Syn-derived
37	MEX94.2.19//SOKOLL/WBLL1			Syn+Lan derived	Syn+Lan derived
38	1447/PASTOR//KRICHAUFF	✖		Elite-Int	Elite
39	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH			Elite	Elite
40	WBLL1*2/KURUKU			Elite	Elite
41	SERI/BAV92			Elite	Elite
42	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH			Elite	Elite
43	WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBLL1			Elite	Elite
44	MUTUS*2/AKURI			Syn-derived	Syn-derived
45	DPW 621-50	✖	✖	Elite	Elite
46	TRCH/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES			Syn-derived	Syn-derived
47	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF			Elite-Int	Elite
48	MEX94.27.1.20/3/SOKOLL//ATTILA/3*BCN/4/PUB94.15.1.12/WBLL1			Syn+Lan derived	Syn+Lan derived
49	SOKOLL//PUB94.15.1.12/WBLL1			Syn+Lan derived	Syn+Lan derived
50	SERI/BAV92//PUB94.15.1.12/WBLL1			Landrace-derived	Landrace-derived
51	SOKOLL//PUB94.15.1.12/WBLL1			Syn+Lan derived	Syn+Lan derived
52	CROC_1/AE.SQUARROSA (224)//OPATA/3/PUB94.15.1.12/WBLL1	✖		Syn+Lan derived	Syn+Lan derived
53	BCN/WBLL1/6/CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC			Elite-Int	Elite
54	SERI/BAV92//JANZ			Elite	Elite
55	OR791432/VEE#3.2	✖	✖	Elite	Elite
56	ATTILA/3*BCN			Elite	Elite
57	SOKOLL			Syn-derived	Syn-derived
58	PASTOR//HXL7573/2*BAU			Elite	Elite
59	SOKOLL/3/PASTOR//HXL7573/2*BAU/4/ASTREB			Syn-derived	Syn-derived
60	SOKOLL/3/PASTOR//HXL7573/2*BAU/4/WBLL4//OAX93.24.35/WBLL1			Syn+Lan derived	Syn+Lan derived
61	WBLL4//OAX93.24.35/WBLL1/5/CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2			Syn+Lan derived	Syn+Lan derived
62	MILAN/KAUZ//DHARWAR DRY/3/BAV92			Landrace-derived	Landrace-derived
63	BAV92/SERI			Elite	Elite
64	PASTOR//HXL7573/2*BAU/3/ATTILA/3*BCN/4/ATTILA/PASTOR			Elite	Elite
65	PUB94.15.1.12/FRTL/5/CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2			Syn+Lan derived	Syn+Lan derived
66	F2SR2-69//YANGLING SHAANXI/PASTOR	✖		Elite	Elite
67	PASTOR//HXL7573/2*BAU/3/WBLL1			Elite	Elite
68	BCN/WBLL1//PUB94.15.1.12/WBLL1			Landrace-derived	Landrace-derived
69	HE1/2*CNO79//BAV92			Elite	Elite
70	CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2			Syn-derived	Syn-derived
71	NAVOJOA M2007			Elite	Elite
72	PASTOR//HXL7573/2*BAU/3/WBLL1			Elite	Elite

#	Pedigree			Class 1	Class 2
73	BABAX/LR42//BABAX/3/ER2000			Elite	Elite
74	SOKOLL/3/PASTOR//HXL7573/2*BAU			Syn-derived	Syn-derived
75	CHWL86/6/FILIN/IRENA/5/CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER			Syn-derived	Syn-derived
76	BECARD			Elite	Elite
77	KACHU			Elite-dur	Elite
78	NELOKI			Elite	Elite
79	PUB94.15.1.12/FRTL	✖		Landrace-derived	Landrace-derived
80	W15.92/4/PASTOR//HXL7573/2*BAU/3/WBLL1			Elite	Elite
81	BECARD/KACHU			Elite	Elite
82	TACUPETO F2001/SAUAL//BLOUK #1			Elite	Elite
83	KUKRI	✖	✖	Elite	Elite
84	D67.2/PARANA 66.270//AE.SQUARROSA (320)/3/CUNNINGHAM/4/VORB			Syn-derived	Syn-derived
85	PVN//CAR422/ANA/5/BOW/CROW//BUC/PVN/3/YR/4/TRAP#1/6/WORRAKATTA/2*PASTOR/7/PRL/2*PASTOR			Elite	Elite
86	BECARD/KACHU			Elite	Elite
87	MUNAL #1			Elite	Elite
88	CNO79//PF70354/MUS/3/PASTOR/4/BAV92*2/5/FH6-1-7	✖	✖	Elite	Elite
89	PBW343*2/KUKUNA*2//FRTL/PIFED			Elite	Elite
90	KACHU #1/4/CROC_1/AE.SQUARROSA (205)//BORL95/3/2*MILAN/5/KACHU			Syn-derived	Syn-derived
91	BABAX/LR42//BABAX/3/VORB			Syn-derived	Syn-derived
92	OR791432/VEE#3.2//ATTILA/3*BCN	✖	✖	Elite	Elite
93	SOKOLL/WBLL1			Syn-derived	Syn-derived
94	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/7/CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO/8/WBLL1*2/KURUKU			Elite-Introgression	Elite
95	CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO/7/BCN/WBLL1/8/C80.1/3*QT4118/KAUZ/RAYON/3/2*TRCH			Elite-Introgression	Elite
96	WBLL1//YANGLING SHAANXI/ESDA/3/ROLF07			Elite	Elite
97	HE1/2*CNO79//BAV92/3/ROLF07	✖		Elite	Elite
98	BCN/WBLL1//PUB94.15.1.12/WBLL1			Landrace-derived	Landrace-derived
99	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/4/BERKUT/KRICHAUFF			Elite-Introgression	Elite
100	WBLL1//PUB94.15.1.12/WBLL1			Landrace-derived	Landrace-derived
101	MEX94.27.1.20/3/SOKOLL//ATTILA/3*BCN			Syn+Lan derived	Syn+Lan derived
102	MTRWA92.161/PRINIA/5/SERI*3//RL6010/4*YR/3/PASTOR/4/BAV92			Elite	Elite
103	SOKOLL/WBLL1			Syn-derived	Syn-derived
104	PRIAMURSKAYA 93/2*TERREMOTO/3/ATTILA/BAV92//PASTOR/4/NAVJ07	✖		Elite	Elite
105	MEX94.27.1.20/3/SOKOLL//ATTILA/3*BCN/4/PUB94.15.1.12/WBLL1			Syn+Lan derived	Syn+Lan derived
106	BCN/WBLL1//ROLF07			Elite	Elite
107	C80.1/3*QT4118//KAUZ/RAYON/3/2*TRCH/7/CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO			Elite-Introgression	Elite
108	TACUPETO F2001/BRAMBLING*2//KACHU			Elite	Elite
109	WBLL1*2/KUKUNA	✖	✖	Elite	Elite
110	WEEBILL1			Elite	Elite

#	Name				
111	ROELFS F2007			Elite	Elite
112	SERI/BAV92//PUB94.15.1.12/WBLL1			Landrace-derived	Landrace-derived
113	SOKOLL/WBLL1	✖	✖	Syn-derived	Syn-derived
114	QUAIU			Elite	Elite
115	BAJ #1			Elite	Elite
116	BORLAUG100 F2014			Elite	Elite
117	VOROBEY	✖	✖	Syn-derived	Syn-derived
118	WBLL4//OAX93.24.35/WBLL1			Landrace-derived	Landrace-derived
119	SOKOLL/WBLL1	✖		Syn-derived	Syn-derived
120	PUB94.15.1.12/WBLL1			Landrace-derived	Landrace-derived
121	WBLL4//OAX93.24.35/WBLL1	✖		Landrace-derived	Landrace-derived
122	BAV92/SERI			Elite	Elite
123	W15.92/4/PASTOR//HXL7573/2*BAU/3/WBLL1			Elite	Elite
124	CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*JANZ/6/MISR2, EGY			Syn-derived	Syn-derived
125	FRANCOLIN #1/WBLL1	✖		Elite	Elite
126	ROLF07*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES			Syn-derived	Syn-derived
127	FRET2/TUKURU//FRET2/3/MUNIA/CHTO//AMSEL/4/FRET2/TUKURU//FRET2			Elite	Elite
128	MUTUS//ND643/2*WBLL1			Elite	Elite
129	MUTUS*2/HARIL #1			Elite	Elite
130	QUAIU*2/KINDE			Elite	Elite
131	DANPHE #1*2/CHYAK			Elite	Elite
132	ND643/2*WBLL1/4/WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBLL1			Elite	Elite
133	MUNAL*2/CHONTE			Elite	Elite
134	CHIBIA//PRLII/CM65531/3/MISR 2/4/MUNAL #1			Elite	Elite
135	NAC/TH.AC//3*PVN/3/MIRLO/BUC/4/2*PASTOR/5/KACHU/6/KACHU			Elite-Int	Elite
136	KACHU #1/4/CROC_1/AE.SQUARROSA (205)//BORL95/3/2*MILAN/5/KACHU	✖	✖	Syn-derived	Syn-derived
137	KACHU//WBLL1*2/BRAMBLING			Elite-durum	Elite
138	KACHU/BECARD//WBLL1*2/BRAMBLING			Elite-durum	Elite
139	SUPER 152			Elite	Elite
140	SUP152*2/TECUE #1			Elite	Elite
141	BECARD/FRNCLN			Elite	Elite
142	FRET2*2/BRAMBLING//BECARD/3/WBLL1*2/BRAMBLING			Elite	Elite
143	KAUZ/PASTOR//PBW343/3/KIRITATI/4/FRNCLN	✖		Elite	Elite
144	WBLL1*2/VIVITSI//AKURI/3/WBLL1*2/BRAMBLING			Syn-derived	Syn-derived
145	SAUAL/3/ACHTAR*3//KANZ/KS85-8-4/4/SAUAL	✖		Elite	Elite
146	JANZ			Elite-Introgression	Elite
147	CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC	✖		Elite-Introgression	Elite
148	CROC_1/AE.SQUARROSA (224)//OPATA			Syn-derived	Syn-derived
149	BCN/RIALTO//ROLF07			Elite	Elite
150	MEX94.27.1.20/3/SOKOLL//ATTILA/3*BCN			Syn+Lan derived	Syn+Lan derived

Table S2. Meteorological data in two seasons (Y16 and Y17) at NW Mexico

		Y16: 2015-16	*Y17: 2016-17*
Booting (GS41-GS49)	Mean Temperature	17.2°C	17.2°C
	Mean Solar radiation	206.1 MJ m^{-2}	194.4 MJ m^{-2}
	Mean Rain accumulated	0.04 mm	0mm
Anthesis (GS59-GS69)	Mean Temperature	18.8°C	17.2°C
	Mean Solar radiation	222.1 MJ m^{-2}	200.0 MJ m^{-2}
	Mean Rain accumulated	0.05 mm	1.6 mm
Grain filling (GS71-GS91)	Mean Temperature	19.7°C	19.1°C
	Mean Solar radiation	242.1 MJ m^{-2}	257.9 MJ m^{-2}
	Mean Rain accumulated	0.17 mm	0.03 mm