1 **Optimizing dry-matter partitioning for increased spike growth, grain number**

2 **and harvest index in spring wheat**

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Abstract

Improving biomass is an important goal for future genetic gains in yield potential in wheat, but it will also be crucial to identify physiological traits to maximize harvest index (HI, proportion of aboveground biomass in grain). Increased grain partitioning will require increased dry-matter (DM) partitioning to the spikes at anthesis as well as enhanced fruiting efficiency (FE, grains per g spike dry matter at anthesis or chaff dry matter at harvest), whilst optimizing the partitioning amongst the non-grain components to maintain post-anthesis photosynthetic capacity and soluble carbohydrate translocation. The objectives of this study were to: i) quantify genetic variation in DM partitioning among plant organs at anthesis (GS65) + 7days and associations with spike growth and FE and ii) identify optimized partitioning traits associated with enhanced HI and grain yield, in CIMMYT elite spring wheat backgrounds. Two field experiments were conducted in 2011-12 and 2012-13 testing 26 CIMMYT spring wheat cultivars in NW Mexico in irrigated conditions in which DM partitioning was assessed in plant organs at anthesis + 7 days, and within-spike (glume, palea, lemma, rachis and awn) partitioning was assessed at harvest. Grain yield, yield components, HI and FE were assessed at harvest. Our results identified new traits for HI (decreased DM partitioning to stem internodes 2 (top down, peduncle -1) and 3, and decreased rachis DM partitioning and rachis specific weight (rachis DM per rachis unit length) and increased lemma DM partitioning), potentially allowing breeders to maximize the exploitation of enhanced carbon assimilation for grain biomass. Further work will focus on understanding the role of soluble carbohydrate re-translocation in these relationships and establishing high-throughput and cost-effective phenotyping methods for these traits for deployment in breeding.

Abbreviations: FE, Fruiting efficiency; SPI, Spike partitioning index; StPI, Stem partitioning index; LPI, Lamina partitioning index; LSPI, Leaf sheath partitioning index; Ped, Peduncle; Int2, Internode 2; Int3, Internode 3; IntR, Internode remainder; DTA, Days emergence to anthesis; GPS Grains per spike; SDM, Spike dry-matter; SPN, Spikes m^{-2}; DTInB, Days from emergence to initiation of booting; SEP, Stem elongation period (days from initiation of booting to anthesis).

1. Introduction

Wheat (*Triticum aestivum* L.) is globally grown on more than 220 million hectares of land with a global average yield of 3.41 t ha^{-1} (FAO 2006). Annual genetic gains for grain yield of wheat in CIMMYT international Elite Spring Wheat Yield Trials from 2007 to 2015 were 0.53% in optimally irrigated environments compared to local checks (Crespo-Herrera et al. 2017). The current annual rate of genetic gain in wheat yield potential from datasets reported globally averages 0.6% (0.3% - 1.1%) (Fischer et al. 2014). However, the rates of yield gains required to meet predicted global demand for cereals in 2050 are higher than the present rates of genetic gains at ca. 1.16% - 1.31% per annum (Hall and Richards 2013). Studies on historic sets of cultivars have shown yield progress has been associated with greater above-ground biomass in the UK (Shearman et al. 2005), Australia (Sadras and Lawson 2011), China (Xiao et al. 2012), Brazil (Beche et al. 2014) and NW Mexico (Aisawi et al. 2015). Some of these studies have shown yield progress was also associated with HI (Xiao et al. 2012; Beche et al. 2014) while others report no systematic progress in HI in the last decades (Shearman et al. 2005; Aisawi et al. 2015). For example, HI has actually decreased in CIMMYT spring wheat cultivars in NW Mexico from 1990 to 2009 (Aisawi et al. 2015). In contrast, in Argentinian wheat cultivars released from 1999-2011 yield progress of 0.18% year^{-1} was associated with an increase in HI of 0.25% year^{-1} with no association with overall above-ground biomass (Lo Valvo et al. 2018). Overall this evidence, combined with the reported co-limitation of grain growth by source and sink during grain filling in modern wheat varieties (Shearman et al. 2005; Acreche and Slafer 2009; Aisawi et al. 2015), indicates that simultaneous increase of photosynthetic capacity and grain partitioning in modern wheat cultivars is a crucial task for breeders. To exploit future genetic gains in biomass for yield potential, it will be necessary to identify traits enabling breeders to discriminate 'useful' and 'non useful' biomass in new high biomass cultivars to maximize partitioning to grain and yield potential gains.

Dry-matter partitioning is the end result of the processes acting on the distribution of dry-matter between the organs of a plant (Marcelis 1996). Biomass accumulated before grain filling is partitioned amongst roots, leaf laminae, leaf sheaths, stems and spikes resulting in competition for assimilate among plant organs. During the stem-elongation phase, stem and spike growth overlaps (Brooking and Kirby 1981) affecting assimilate supply to the spike (Slafer and Rawson 1994) which determines floret survival and the final number of grains per spike (Fischer, 1985; Fischer and Stockman, 1986; Kirby, 1988; Siddique, Kirby and Perry, 1989; Slafer, Andrade and Satorre, 1990). The hypothesis that these processes compete for assimilates is supported by the fact that reductions in plant height associated with the *Rht-B1b* (formerly *Rht1*) and *Rht-D1b* (formerly *Rht2*) alleles

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increased spike DM, grains m^{-2} and HI (Gale and Youssefian, 1985; (Flintham et al. 1997) at the expense of stem dry matter (Fischer 1985).

One approach to increase spike growth at anthesis, hence grains m^{-2}, is by increasing the relative durations of the phenological stages involved in spike growth (Miralles et al. 2000; Slafer et al. 2005; Gonzalez et al. 2011). Alternatively, decreases in partitioning to non-spike organs (stems, leaf laminae and leaf sheaths) can be targeted to favour partitioning to the spike, independently of changes in phenology (Foulkes et al. 2011). This must, however, take account of any effects of reduced leaf-lamina and/or leaf-sheath partitioning on photosynthetic capacity; or of reduced stem partitioning on retranslocation of stored carbohydrates to grain, and mechanical strength of the stem in relation to lodging resistance.

Since stem and spike growth overlaps during stem elongation mainly during the rapid spike growth phase from booting to anthesis (Brooking and Kirby 1981), the extent of competition between the spike and stem should differ between stem internodes. The timing of maximum stem growth rates has been reported to vary from 11-17 days before anthesis to around anthesis (Borrell et al. 1989, 1991; Youssefian et al. 1992), i.e., when both the peduncle and the penultimate internode are rapidly extending (Youssefian et al. 1992). However, maximum stem length is usually reached after anthesis (Borrell et al. 1989; Youssefian et al. 1992; Bonnett and Incoll 1992; Ehdaie et al. 2006), with post-anthesis stem extension attributed solely to peduncle extension. Genetic variation in stem-internode partitioning has been reported in association with stem dry-matter loss and grain growth (Borrell et al. 1993; Ehdaie et al. 2006) in studies comparing tall versus semi-dwarf cultivars, but to our knowledge not previously in elite semi-dwarf cultivars directly related to pre-anthesis spike growth.

The complementary trait to spike partitioning and spike growth to enhance grain number and HI is the fruiting efficiency (FE, number of grains per unit spike dry-matter at anthesis or chaff dry-matter at harvest). To date there is no strong evidence for the direct use of this trait in breeding for yield potential (Slafer et al. 2015; Lo Valvo et al. 2018); although wide genetic variation has been reported among modern wheat cultivars (González et al. 2011; Lázaro and Abbate 2011; Mirabella et al. 2015; Elía et al. 2016; Gonzalez-Navarro et al. 2016). Results on a spring wheat Bacanora × Weebil DH population suggested that strategic crossing of two high yielding lines of a breeding program may be a valuable strategy to increase further grain number through the expression of transgressive variation in fruiting efficiency (Garcia et al., 2014). There may be potential trade-offs between FE and spike dry-matter partitioning (Lázaro and Abbate 2011; Ferrante et al. 2012; Gaju et al. 2014), but cultivars that can combine high FE with high SPI and spike dry matter have been

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identified (Bustos et al. 2013; García et al. 2014). However, to date, strategies to increase FE that do not involve changes in phenology have not been investigated extensively. It has been suggested that improvements in fruiting efficiency could be associated with better intra-spike partitioning with a concomitant increase in biomass being delivered to developing florets instead of structural components of the spike (Slafer and Andrade 1993; García et al. 2014), or to florets of smaller size (Dreccer et al., 2009). One possible avenue to increase FE may be through more optimized DM partitioning within the spike structural components (glumes, paleas, lemmas, rachis or awns) (Abbate et al., 1998; Foulkes et al., 2011; Slafer et al., 2015). Abbate et al. (1998) suggested that a smaller rachis dry weight in proportion to spike dry weight could result in higher FE.

In this study, we examined dry-matter partitioning amongst the plant organs at anthesis (spike, stem and internodes, leaf lamina and leaf sheath) and physiological maturity (grain, spike (chaff) structural components and straw) and associations with key harvest traits in 26 CIMMYT elite spring wheat cultivars in two field experiments under irrigated high potential conditions in NW Mexico. The objectives were to: i) quantify genetic variation in dry-matter partitioning among plant organs seven days after anthesis and associations with spike growth and FE and ii) identify optimized partitioning traits associated with enhanced HI and grain yield in CIMMYT elite spring wheat backgrounds.

2. Materials and Methods

2.1. Plant material and experimental conditions and design

Two field experiments were conducted at the CIMMYT research station (Campo Experimental Norman E. Borlaug; CENEB) in 2011-12 and in 2012-13 (hereafter referred to as 2012 and 2013, respectively) in the Yaqui Valley near Ciudad Obregon, Sonora (27° N, 110° W; 38 m.a.s.l.), NW Mexico under fully irrigated conditions. The soil is coarse sandy clay; mixed montmorillonitic typic caliciorthid, low in organic matter and slightly alkaline (pH 7.7) (Sayre et al. 1997). Twenty-six spring wheat cultivars were grown using a randomised complete block design with three replications. Each plot consisted of two raised beds with an additional bed between plots to avoid border effects, each of which was 8.5 m long and 0.80 m wide with two rows (24 cm gap between rows). The experiments were sown on 8 December 2011 and 23 November 2012. The seed rate was 108 and 110 kg ha^{-1} in 2012 and 2013, respectively (equivalent to *ca.* 270 and 275 seeds m^{-2}, respectively).

In each season, the previous crop was wheat after a summer fallow. Each year the plots were irrigated six to seven times during the crop cycle at intervals of 3 to 4 weeks. In 2012, crop emergence occurred on 16 December and irrigation was applied seven times, including the irrigation

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after sowing. In 2013, the emergence date was 2 December 2012 and six irrigations were applied. The first application of nitrogen (N) (50 kg N ha^{-1}) was applied as urea during land preparation, followed by 40 kg ha^{-1} of phosphorous (P) as triple super phosphate at sowing. The second application of nitrogen (150 kg N ha^{-1}) as urea was added at the time of first irrigation. In both years, Buctril (Bayer AG; a.i. 3, 5-dibromo-4-hydroxybenzonitrile) and Starane (Dow AgroSciences LLC; a.i. fluoroxypyr) were applied as herbicides for broad and narrow leaves weeds, respectively, as required. Folicur (Bayer AG; a.i. tebuconazole) was applied as fungicide three times per season. Muralla (Bayer AG; a.i. imacloprid + betacyfluthrin) was applied as insecticide as required. No plant growth regulators were applied. The 26 spring wheat cultivars were selected from the CIMMYT breeding program, comprising part of the CIMMYT Mexico Core Germplasm (CIMCOG) panel (Table 1). The CIMCOG cultivars were mainly modern high yield CIMMYT releases and advanced lines with high biomass expression together with a small number of historic releases which have been widely distributed and grown worldwide. All the cultivars were semi-dwarf cultivars and photoperiod insensitive. The classifications of the cultivars according to allelic expression of the *Ppd-D1 gene* for photoperiod insensitivity and for the *Rht-D1* and *Rht-B1* semi-dwarf genes for plant height are given in Table 1.

Season and long-term data for daily mean air temperature, daily mean solar radiation and accumulated monthly rainfall were collected from a weather station located 1-2 km from the field experiments (Table 2). Mean air temperature during December (~GS10-GS29) was 2.7 ºC colder in 2012 compared to 2013. During January, February and March (GS31-early grain filling), mean air temperature was 1.7 ºC colder in 2012 than in 2013. Mean air temperature during most of late grain filling was similar in both years, but slightly warmer in 2012 (+0.6 ºC). Mean solar radiation was similar in both seasons for most months, with the exception of April, having 3.5 MJ m^{-2} day^{-1} more in 2012 than in 2013. Accumulated rainfall was similar during pre-anthesis (December-February) and grain filling (March-April) in both seasons.

Table 1. Code number, year of release (YoR) and cultivar name for the 26 cultivars in the CIMCOG panel in 2012 and 2013 at Cd. Obregon. NW Mexico. Historic cultivars are shaded. Cultivars in bold represent the selection for the non-grain spike dry-matter partitioning analysis. Reduced height *Rht-B1a/Rht-B1b*, *Rht-D1a/Rht-D1b*, and photoperiod insensitivity *Ppd-D1a/Ppd-D1b* classes, and average days to anthesis (DTA; days after emergence, DAE) and plant height (PH) of 26 CIMCOG cultivars. Values represent means in 2012 and 2013. The *Rht-B1b* and *Rht-D1b* alleles confer semi-dwarf stature and the *Ppd-D1a* allele confers insensitivity to photoperiod.

Code	YoR	Cultivar name	*Rht-D1*	*Rht-B1*	*Ppd-D1*	PH (cm)	DTA (DAE)
1	**1992**	**BABAX/LR42//BABAX/3/VORB**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	114.6	86.7
2	**1999**	**BACANORA T 88**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	91.6	86.3
3	2001	BCN/RIALTO	*Rht-D1b*	*Rht-B1a*	*Ppd-D1a*	83.5	97.0
4	**2003**	**BECARD/5/KAUZ//ALTAR 84**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	105.3	90.8
5	**2003**	**BRBT1*2/KIRITATI**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	109.9	83.0
6	2005	SAUAL/4/CROC_1/AE.SQUARROSA	-	-	-	110.5	92.5
7	**2005**	**SAUAL/WHEAR//SAUAL**	-	-	-	105.9	86.0
8	**2005**	**CMH79A.955/4/AGA**	*Rht-D1b*	*Rht-B1a*	*Ppd-D1a*	101.3	94.7
10	2006	CNO79//PF70354/MUS/3	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	111.8	85.2
11	2006	CROC_1/AE.SQUARROSA	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	106.8	83.0
12	2006	KBIRD//INQALAB 91*2	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	105.8	93.3
13	2007	MILAN/KAUZ//PRINIA	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	107.9	83.0
14	**2008**	**PAVON F 76**	*Rht-D1b*	*Rht-B1a*	*Ppd-D1a*	103.7	86.7
15	**2008**	**PBW343*2/KUKUNA*2**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	104.1	84.2
16	2008	PFAU/SERI.1B//AMAD/3	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	105.5	77.0
17	**2009**	**SERI M 82**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	95.9	87.5
18	**2009**	**SIETE CERROS T66**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	102.7	82.5
19	2009	SOKOLL//PBW343*2	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	106.1	86.3
20	2009	TACUPETO F2001/7/CAL/NH	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	111.8	84.5
21	**2009**	**TACUPETO F2001/BRAMBLING**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1b*	104.2	88.2
22	**2009**	**TC870344/GUI**	-	-	-	116.2	84.5
23	**2009**	**TRAP#1/BOW/3/VEE/PJN**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	109.8	84.7
24	**2009**	**UP2338*2/4/SNI/TRAP#1/3**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	105.5	89.5
25	**2009**	**BECARD**	-	-	-	105.6	83.0
26	**2009**	**WBLL1*2/KURUKU*2/5/REH**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	108.4	91.3
27	**2009**	**YAV_3/SCO/JO69/CRA/3**	*Rht-D1a*	*Rht-B1b*	*Ppd-D1a*	109.1	88.5

Table 2. Environmental conditions at the experimental site for each field season (2012 and 2013) during the wheat cycle and 17-year long-term mean (LTM: 1997-2013). Monthly mean maximum and minimum temperatures are in parenthesis.

	Month	2011-12	2012-13	LTM
Air temperature (°C)	Dec	13.7 (24.1-4.8)	16.4 (25.0-9.6)	15.4 (24.9-7.6)
Monthly daily mean (max-min)	Jan	15.3 (27.0-6.2)	14.1 (23.7-6.5)	14.9 (24.9-6.7)
	Feb	15.1 (24.6-7.4)	14.0 (23.8-5.9)	15.3 (25.1-7.3)
	Mar	16.8 (27.0-8.2)	18.5 (29.1-9.5)	17.3 (27.5-8.4)
	Apr	20.2 (30.7-10.9)	19.6 (29.3-11.1)	20.3 (30.5-10.8)
Solar radiation (MJ m^{-2})	Dec	14.4	12.4	14.3
Daily mean	Jan	14.8	14.8	15.1
	Feb	18.0	16.9	18.6
	Mar	22.2	20.6	23.2
	Apr	26.2	22.7	26.2
Mean rainfall (mm)	Dec	0.25	10.62	7.64
Accumulated per month	Jan	0	1.76	15.68
	Feb	13.7	0.50	9.24
	Mar	0	1.50	1.55
	Apr	0.25	1.0	1.25

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2.3. Crop measurements

Unless otherwise stated, measurements were carried out in all 26 cultivars. In each experiment, plants were counted in each plot shortly after emergence in a 0.8 m^2 area. Dates of initiation of booting (GS41), onset of anthesis (GS65) (Zadoks et al. 1974) and physiological maturity (GS89) (50% of the peduncle with a yellow colouration) were recorded for each plot, when 50% of the shoots in the plot were at the stage. Plant height to the tip of the spike was recorded at four positions in each plot shortly before physiological maturity. In both years, in each plot plant material was sampled at anthesis +7 days (GS65+7) (samples taken on actual date of reaching the stage) in an area of 0.8 m^2 (four 50 cm length rows, 1.6 m total width) by cutting at ground level. A sub-sample consisting of 100 shoots was taken and the weight recorded before and after oven drying at 70°C for 48 h to constant weight. Before oven drying, infertile shoots (those without an emerged spike) were counted in the sub-sample; the remaining shoots were classified as fertile. From the remaining sample, ten randomly selected fertile shoots were separated into: i) leaf lamina ii) leaf sheath, iii) stem and iv) spike. The weight of each plant component was recorded after drying at 70°C for 48 h to constant weight. The DM partitioning indices of each component (lamina partitioning index, LPI; leaf sheath partitioning index, ShPI; stem partitioning index, StPI and spike partitioning index, SPI) were calculated as the ratio of plant component DM/aboveground DM. In addition, the ten stems (iii) were further separated into their phytomers, peduncle (Ped), internode 2 (Int2), internode 3 (Int3) and internode remainder (IntR). Internode lengths were recorded. After oven drying at 70°C for 48 h to constant weight, dry weights were recorded separately for each internode. The DM partitioning indices of each internode were calculated as the ratio of internode DM/aboveground DM (peduncle DM partitioning index, Ped PI; internode 2 DM partitioning index, Int2 PI; internode 2 DM partitioning index, Int3 PI and internode remainder DM partitioning index, IntR PI). Internode specific weight (SW) was calculated by dividing the internode DM shoot^{-1} by the internode length (cm) and is expressed as mg cm^{-1} for each internode (Ped SW, Int2 SW, Int3 SW and IntR SW).Fruiting efficiency was calculated based on the spike DM per m^2 at GS65+7 days (FE$_A$) and also based on the chaff DM per m^2 at harvest (non-grain spike DM) (FE$_H$), by dividing the grains m^{-2} at harvest by the spike or chaff DM (g m^{-2}). After physiological maturity, grain yield was measured in each plot by machine-harvesting an average plot area of 5.7 m^2 and 4.8 m^2 in 2012 and 2013, respectively, and values adjusted to 15% moisture. Prior to that, a random sample of 100 fertile shoots was taken at physiological maturity, cutting shoots at ground level. The plant material was oven dried for 48 h at 70°C to constant weight, weighed, then threshed and the grain collected and weighed. From this lot, 200 grains were randomly counted and weighed. Using these data, harvest

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228   index (proportion of above-ground DM as grain; HI), above-ground dry-matter (AGDM$_H$) and yield

229   components at harvest were calculated.

230   Finally, 17 of the 26 genotypes (3, 6, 10, 11, 12, 13, 16, 19 and 20 not assessed; see Table 1 for

231   cultivar names) were selected for a detailed non-grain spike partitioning analysis. The rationale for

232   the selection of the lines was to represent the full range for FE with a restricted range of anthesis

233   date. For this analysis, three spikes were randomly selected before harvest in 2012 and 2013 and

234   dissected into: i) glumes, ii) lemmas, iii) paleas, iv) rachis and v) awns. The different spike

235   components and grains were bulked for the three spikes and weighed separately after drying at 70°C

236   for 48 h to constant weight. The number of grains was counted for the three spikes. The non-grain

237   spike DM partitioning was calculated as the ratio of spike component DM/non-grain spike DM. In

238   2013, rachis length was also measured for each of the three spikes and the rachis specific weight

239   calculated by dividing the rachis dry weight by the rachis length.

240   *2.3. Statistical analysis*

241   The means for each year, combined years and cultivars for all the traits are adjusted means

242   estimated using the General Linear Model (GLM) procedure from META R 6.0 (Alvarado et al.,

243   2017) that uses a suite of R codes (R 3.3.1 was used to run the suite of codes). Replications, years,

244   genotypes and genotype per year interactions (GxY) were considered as random effects. A covariate

245   for anthesis date as a fixed effect was included in the analyses of variance when this had a significant

246   effect, with the exception of other phenological traits such as physiological maturity date (days from

247   emergence to maturity). Least significant differences (LSD$_{0.05}$) between traits means were calculated.

248   Procedures to estimate cross-year broad-sense heritability (H^2) of a given trait were also

249   implemented using the META R software, calculated as described in Equation 1 (Cooper et al.,

250   1996).

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{re}}$$

251   (1)

252   Where σ_g^2 and σ_e^2 are the genotypic and error variance, σ_{ge}^2 is the cultivar x environment

253   interaction. The number of environments and number of replicates are represented by *e* and *r*,

254   respectively.

255   Linear and non-linear regression analysis was applied to two-year genotype means for selected

256   traits. All correlations among traits presented in this study are genetic correlations (r_g) and were

257   calculated for cross-year means as described in Equation 2 (Cooper et al. 1996):

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$$r_{\mathrm{g}} = \frac{\overline{\sigma_{\mathrm{g}(JJ')}}}{\overline{\sigma_{\mathrm{g}(J)}\sigma_{\mathrm{g}(J')}}}$$

258   (2)

259   where $\overline{\sigma_{\mathrm{g}(JJ')}}$ is the adjusted mean of all pairwise genotypic covariances between trait j and j' and

260   $\overline{\sigma_{\mathrm{g}(J)}\sigma_{\mathrm{g}(J')}}$ is the average of all pairwise geometric means among the genotypic variance components

261   of the traits.

262   A forward stepwise multiple linear regression was applied to genotype means with spike

263   partitioning index (SPI) and harvest index (HI) as the dependent variables and plant height, peduncle

264   length, Int2 length, Int3 length, Ped PI, Int2 PI, Int3 PI, Ped SW, Int2 SW, Int 3 SW and $AGDM_{A7}$

265   as independent variables using the cross-year means in Genstat 18th Edition (VSN International

266   2015). The adjusted R^2 statistic values are presented calculated as: $100 \times (1 - (\text{residual mean}$

267   square/total mean square)).

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269   **3. Results**

270   *3.1. Grain yield and harvest traits in CIMCOG cultivars*

271   Averaging over 2012 and 2013, grain yield in the CIMCOG panel ranged from 593 to 740 g m^{-2}

272   ($P <0.01$). There was wide genetic variation also for aboveground dry-matter at harvest ($AGDM_H$),

273   harvest index (HI), yield components, phenological stages and plant height ($P <0.001$; Table 3).

274   High values of heritability were observed for most traits (0.71 – 0.96) for the combined analysis

275   across years (Table 3). Grain yield was positively and linearly associated with $AGDM_H$ ($R^2 =0.59$, P

276   <0.001; Fig. 1a) and non-linearly with HI ($R^2 =0.26$, $P <0.01$; Fig. 1b). Results showed a trade-off

277   between HI and $AGDM_H$ ($R^2 =0.17$, $P <0.05$; Fig. 1c).

278   Genetic correlations between key harvest and partitioning traits among the 26 CIMCOG cultivars are

279   shown in Table 4. Grain yield was not associated significantly with either grains m^{-2} (GN) or

280   thousand grain weight (TGW) among the 26 cultivars (Table 3), presumably related to a strong

281   negative association between these yield components ($r =0.92$, $P <0.001$). While plant height was

282   not associated with grain yield (Fig. 1d), it was negatively correlated with GN ($r =-0.85$, $P <0.001$)

283   and positively with TGW ($r =0.86$, $P <0.001$) (Table 4). In contrast, days to anthesis (DTA) was

284   positively correlated with GN ($r =0.50$, $P <0.01$) and negatively with TGW ($r =-0.41$, $P <0.05$).

285   These latter effects may have related in part to later anthesis increasing radiation interception in the

286   pre-anthesis phase hence grains m^{-2}, in turn, tending to decrease TGW. As expected, spikes m^{-2} at

287   harvest (SPN) had a positive effect on GN ($r =0.72$, $P <0.001$) and a negative effect on TGW ($r =-$

288   0.67, $P <0.001$) and grains per spike (GPS) ($r =-0.45$, $P <0.05$) (Table 4). Fruiting efficiency was

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289 higher when calculated using chaff DM at harvest (FE$_H$; 68.2-118.3 grains g^{-1}) than when using spike

290 dry-matter at GS65+7d (SDM) (FE$_A$; 52.4-82.9 grains g^{-1}) (Table 3). Grains m^{-2} showed a positive

291 linear association with spike DM at GS65+7d (SDM, g m^{-2}) (R^2 =0.30, P <0.01; Fig. 2a) but was not

292 related to the spike partitioning index (spike DM/aboveground DM; SPI) (Fig. 2b). FE$_A$ and FE$_H$

293 were both strongly positively associated with GN (R^2 =0.84, P <0.00 and R^2 =0.40, P <0.001,

294 respectively; Fig. 2c).

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296 **Table 3**. Harvest traits and phenological stages for the 26 CIMCOG cultivars. GY: grain yield (100% DM),

297 TGW: thousand grain weight, HI: harvest index, AGDM$_H$: aboveground DM at harvest, GN: grains m^{-2}, SPN:

298 spikes m^{-2}, GPS: grains per spike, DTA: days from emergence to anthesis, DTM: days from emergence to

299 maturity, PH: plant height (PH), Chaff$_H$: chaff DM at harvest, FE$_H$: fruiting efficiency calculated with chaff

300 DM at harvest and FE$_A$: fruiting efficiency calculated with spike DM at GS65+7 days (FE$_A$). Values represent

301 means of 2012 and 2013.

Trait	GY	TGW	HI	AGDM$_H$	GN	SPN	GPS	DTA	DTM	PH	Chaff$_H$	FE$_A$	FE$_H$
	g m^{-2}	g	.	g m^{-2}	m^{-2}	m^{-2}		Days	Days	cm	g m^{-2}	grain	grains g^{-1}
Mean	679.2	42.5	0.48	1421	16224	297	55.4	87	130	105.5	196.5	62.1	83.8
Maximum	739.6	50.7	0.51	1548	22288	401	72.1	97	136	116.2	227.0	82.9	118.3
Minimum	592.8	32.4	0.45	1283	13301	236	44.3	77	124	83.5	178.2	52.4	68.2
Mean 2012	674.3	41.7	0.46	1465	16370	296	56.4	87	130	104.1	217.7	60.1	75.9
Max 2012	742.0	50.0	0.49	1623	23071	396	72.1	94	136	114.9	244.4	79.8	111.3
Min 2012	594.4	31.4	0.43	1310	13324	212	45.8	81	124	83.3	195.9	48.9	64.9
Mean 2013	684.2	43.3	0.50	1377	16078	298	54.4	87	129	106.9	175.2	64.4	92.0
Max 2013	756.3	53.2	0.53	1493	23761	407	74.7	100	138	117.5	209.6	77.0	136.3
Min 2013	591.2	29.8	0.46	1241	12494	239	42.7	73	123	83.8	157.0	46.3	70.8
h^2 [a]	0.71	0.96	0.86	0.76	0.9	0.84	0.82	0.81	0.84	0.96	0.69	0.77	0.93
CV [b]	5.3	5.1	3.2	5.6	7.0	9.4	9.7	1.4	1.8	2.5	7.4	12.5	7.5
LSD Gen. [c]	30.8	2.78	0.01	102.9	1935	48.7	7.72	5.59	3.91	4.65	19.4	10.7	8.78
Prob. Gen.	**	***	***	***	***	***	***	***	***	***	***	***	***
Prob. Y	ns	*	***	*	ns	Ns	ns	Ns	Ns	***	***	ns	***
Prob. GxY	ns	ns	ns	ns	ns	**	ns	***	*	*	Ns	ns	ns

302 [a]: broad sense heritability.

303 [b]: coefficient of variation.

304 [c] LSD Gen.: Least significance difference (5%).

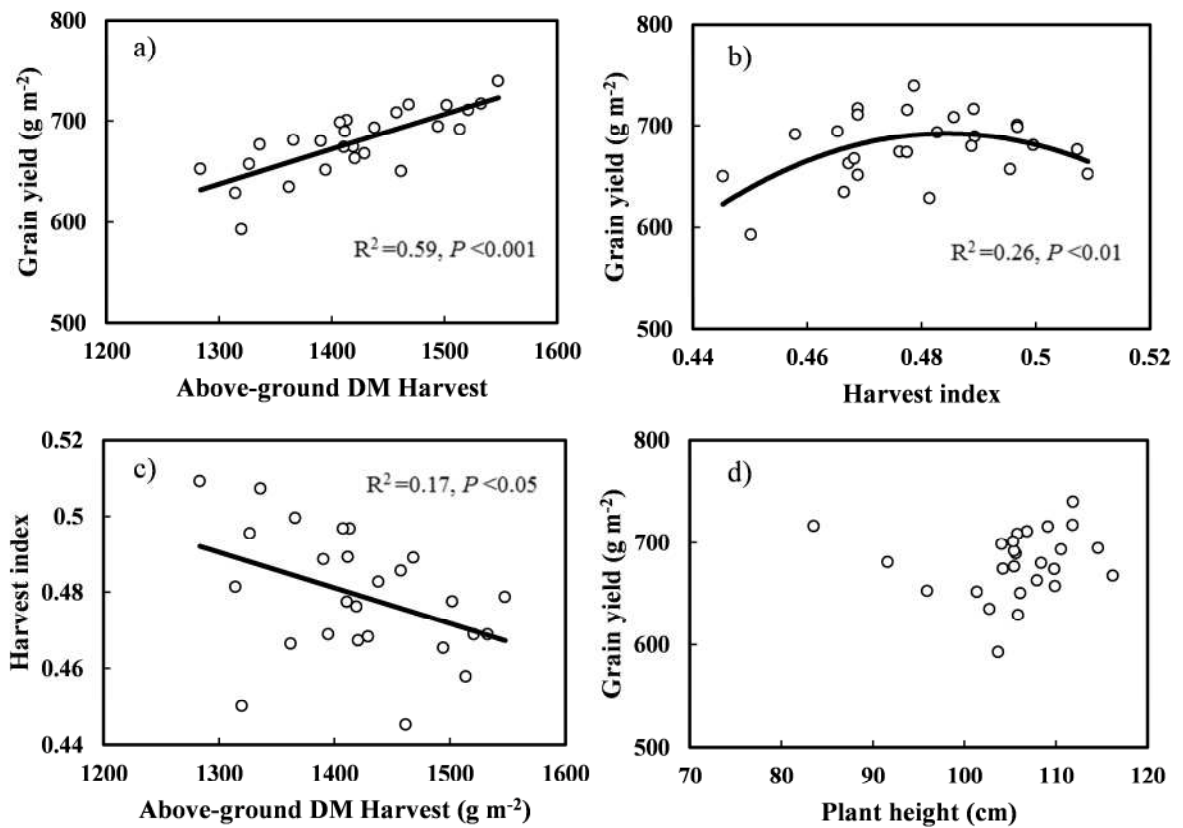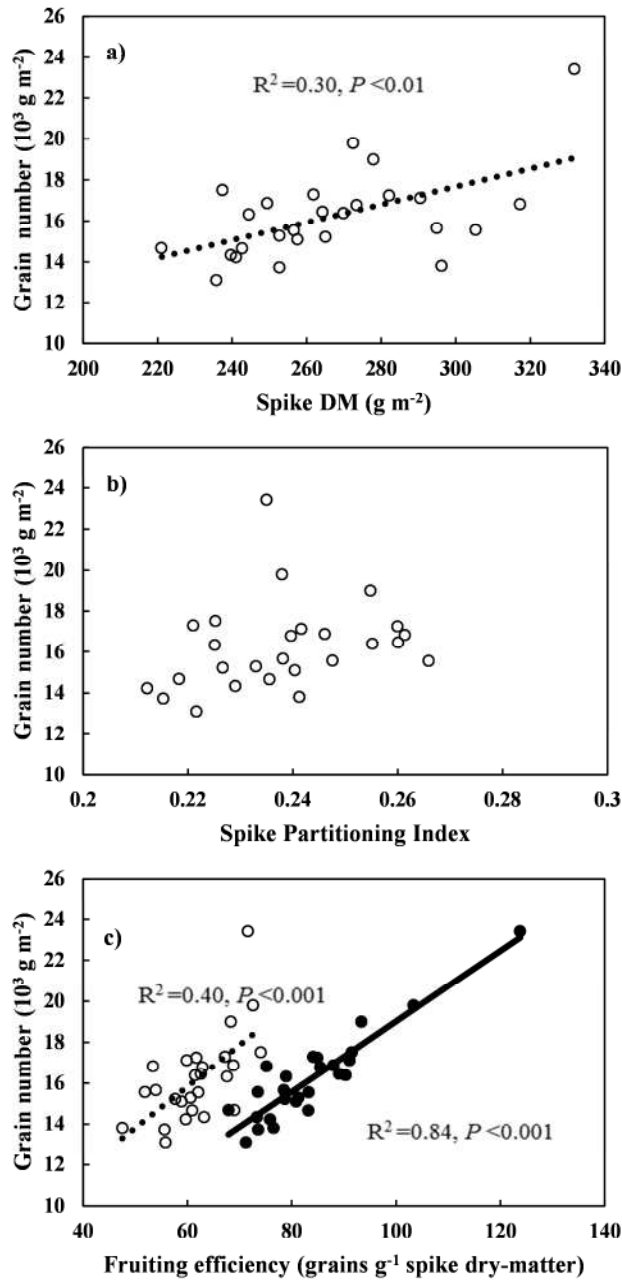305 Probabilities: *P < 0.05; **P < 0.01; ***P < 0.001 and ns (not significant).

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Figure 1. Regression among the 26 CIMCOG cultivars of a) grain yield (100% DM) on above-ground dry-matter (AGDM) at harvest, b) grain yield on harvest index, c) harvest index on AGDM at harvest and d) grain yield on plant height. Values represent means in 2012 and 2013.

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Figure 2. Linear regressions among the 26 CIMCOG cultivars for grains m^{-2} (GN) on a) spike dry-matter (g m^{-2}) at GS65 + 7days, b) spike partitioning index and c) fruiting efficiency (grains per gram of spike dry-matter m^{-2}). In c), open symbols are for FE calculated with spike dry matter at anthesis (GS65) +7 days m^{-2} (FE$_A$) and closed symbols are for FE calculated with chaff dry matter m^{-2} at harvest (FE$_H$). Values represent means in 2012 and 2013.

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3.2. Genetic variation in dry-matter partitioning at anthesis

The aboveground DM at GS65+7d differed among the 26 cultivars (Table 5), and showed no significant correlation with $AGDM_H$ (r =-0.36, P >0.1; Table 4). Spike DM at GS65+7d (SDM) ranged from 226 to 314 g m^{-2} (P <0.001) (Table 5). Although there was variation for spike number m^{-2} at GS65+7d (236 - 401, P <0.001; Table 3), differences in SDM (g m^{-2}) were associated with spike DM per shoot (R^2=0.46, P <0.05) rather than spikes per m^2 (ns). There were significant differences among cultivars in the DM partitioning to the spikes, stems, leaf laminae and leaf sheaths. Averaged across years, spike partitioning index ranged from 0.21 to 0.26 (P <0.001, Table 5, Fig. 3) and the stem DM partitioning index from 0.32 to 0.41 amongst the 26 cultivars (P <0.001, Fig. 3). Lamina DM partitioning index and leaf-sheath DM partitioning index showed similar values, with ranges of 0.18-0.23 and 0.16-0.20 (P <0.001), respectively (Fig. 3). Dry-matter amounts for the different plant components (Fig. 3) ranged from 356-482 g m^{-2} for stems, 221-332 g m^{-2} for spikes, 181-326 g m^{-2} for the laminae and 163-275 g m^{-2} for leaf sheaths (P <0.001) amongst the 26 cultivars.
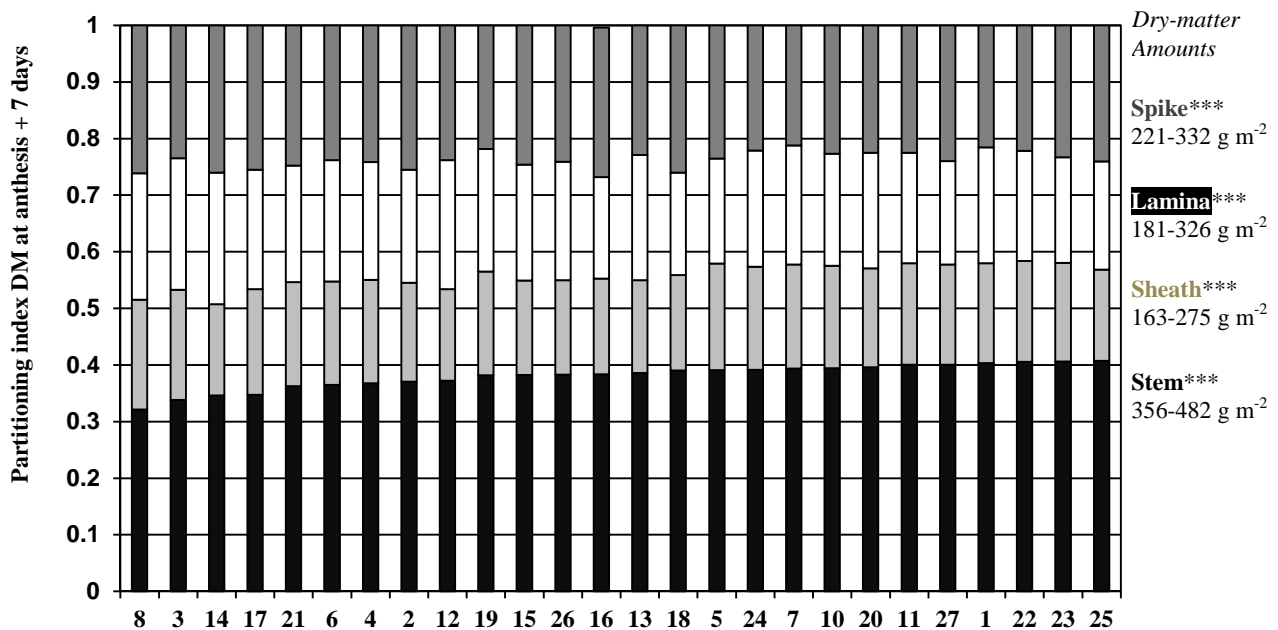
Figure 3. Dry-matter partitioning indices and dry-matter amounts for each plant component for the 26 CIMCOG cultivars at GS65+7d. Values represent means in 2012 and 2013.

Stem (h^2 =0.74; LSD=0.033, *P-value* Gen. <0.001), Leaf sheath (h^2 =0.55, LSD Gen.=0.019, *P-value* Gen. <0.01), Leaf lamina (h^2 =0.83, LSD Gen.=0.018, *P-value* Gen. <0.001) and spike (h^2 =0.78; LSD Gen.=0.020, *P-value* Gen. <0.001).

h^2: broad sense heritability.

LSD: Least significance difference (5%);

Prob. Gen: Probability for genotype.

Probabilities: *P < 0.05; **P < 0.01 and ***P < 0.001.

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Table 4. Genetic correlations between dry-matter (DM) partitioning related traits at GS65+7 days and key harvest traits among the 26 CIMCOG cultivars (based on cross-year means in 2012 and 2013). GY: grain yield, TGW: thousand grain weight, HI: harvest index (HI), $AGDM_H$: aboveground DM at harvest, GN: grains m^{-2}, SPN: spikes m^{-2}, GPS: grains per spike, DTA: days from emergence to anthesis, DTM: days from emergence to maturity, PH: plant height (PH), FE_H: fruiting efficiency calculated with chaff DM at harvest, FE_A: fruiting efficiency calculated with spike DM at GS65+7 days, $AGDM_{A7}$: aboveground DM at GS65+7 days, SDM: spike DM at GS65+7 days, SPI: spike partitioning index, StPI: stem partitioning index, LPI: lamina partitioning index and ShPI: sheath partitioning index. Values in bold indicate significant correlation (at $P <0.05$). Italic values indicate correlation significance is $P <0.1$

Traits	GY	TGW	HI	$AGDM_H$	GN	SPN	GPS	DTA	PH	FE_H	FE_A	$AGDM_{A7}$	SDM	SPI	StPI	LPI	ShPI
GY	-																
TGW	0.14	-															
HI	0.29	-0.14	-														
$AGDM_H$	**0.72**	0.22	**-0.46**	-													
GN	0.21	**-0.92**	0.24	0.03	-												
SPN	0.06	**-0.67**	0	0.07	**0.72**	-											
GPS	0.15	-0.27	0.28	-0.06	0.29	**-0.45**	-										
DTA	0.11	**-0.41**	-0.06	0.14	**0.50**	0.03	**0.63**	-									
PH	0.1	**0.86**	*-0.37*	*0.35*	**-0.85**	**-0.57**	-0.3	**-0.45**	-								
FE_H	0.31	**-0.81**	**0.47**	-0.07	**0.95**	**0.82**	0.06	**0.39**	**-0.79**	-							
FE_A	0.31	**-0.71**	0.04	0.28	**0.79**	**0.99**	**-0.43**	-0.03	**-0.46**	**0.77**	-						
$AGDM_{A7}$	**0.43**	*-0.33*	0.02	*0.36*	**0.59**	0	**0.76**	**0.99**	**-0.54**	**0.49**	0.04	-					
SDM	0.02	**-0.62**	0.22	-0.09	**0.66**	-0.30	**0.88**	**0.78**	**-0.92**	**0.49**	0.19	**0.91**	-				
SPI	**-0.53**	**-0.55**	**0.46**	**-0.78**	0.31	-0.07	**0.52**	-0.06	**-0.48**	0.31	-0.05	-0.16	**0.43**	-			
StPI	**0.46**	**0.72**	-0.06	**0.51**	**-0.55**	-0.01	**-0.74**	**-0.85**	**0.71**	**-0.47**	-0.06	**-0.57**	**-0.97**	**-0.61**	-		
LPI	-0.19	**-0.42**	-0.26	0	**0.39**	0.2	0.27	**0.76**	**-0.40**	0.32	0.15	**0.44**	**0.60**	-0.08	**-0.72**	-	
ShPI	0.15	-0.16	0.06	0.14	0.28	-0.16	**0.64**	**0.72**	*-0.35*	0.15	-0.20	**0.96**	**0.85**	-0.20	-0.25	0.09	-

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Plant height was negatively correlated with $AGDM_{A7}$ ($r =-0.54$, $P <0.01$) and with SPI ($r =-0.48$, $P <0.05$) and positively with StPI ($r =0.71$, $P <0.001$) (Table 4). Moreover, a later DTA had a negative effect on StPI, a positive effect on LPI and ShPI and no effect on SPI (Table 4). There was no effect of spikes m^{-2} on $AGDM_{A7}$ or on the DM partitioning indices or amounts in the spike, stem, leaf sheaths or lamina (Table 4).

Dry-matter partitioning within the stem was assessed in order to identify the internode sections associated most strongly with spike DM partitioning and growth. Averaging over years and cultivars, internode DM $shoot^{-1}$ differed ($P <0.001$) decreasing from the top to the base of the stem: peduncle DM (Ped, 405 mg), internode 2 DM (Int2, i.e. peduncle -1, 319 mg), internode 3 DM (Int3, 249 mg) and internode remaining DM (IntR, 333 mg) (Table 6). Figure 4 shows mean values and ranges for

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377   stem internode DM partitioning indices (stem internode DM / aboveground DM). Peduncles

378   accounted for the most stem DM (31%), representing 11.8% of aboveground DM (P <0.001). Int2,

379   Int3 and IntR represented 25.5, 19.1 and 24.4% of stem DM and 9.3, 7.3 and 9.7% of $AGDM_{A7}$,

380   respectively (P <0.001).

381

382   **Table 5**. Mean, maximum and minimum values for aboveground dry-matter

383   ($AGDM_{A7}$), spikes per m^2, spike partitioning index (SPI) and spike DM per m^2

384   (SDM) at GS65+7 days for the 26 CIMCOG cultivars in 2012 and 2013.

|	$AGDM_{A7}$	Spikes	SDM	SPI
	g m^{-2}	m^{-2}	g m^{-2}	
Mean	1115	444	267	0.238
Maximum	1415	574	314	0.264
Minimum	926	348	226	0.212
Mean 2012	1102	455	275	0.247
Max 2012	1249	579	317	0.276
Min 2012	942	333	229	0.220
Mean 2013	1126	433	260	0.229
Max 2013	1582	568	328	0.277
Min 2013	879	362	202	0.199
$h^{2\,a}$	0.52	0.87	0.25	0.78
$CV^{\,b}$	9.9	10.0	12.3	5.9
LSD Gen.^{c}	209	63.6	49.1	0.021
Prob Gen.	***	***	***	***
Prob. Y	**	ns	ns	*
Prob. GxY	ns	ns	ns	ns

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386   [a] broad sense heritability.

387   [b] *CV*.: coefficient of variation.

388   [c] *LSD* Gen.: Least significance difference (5%).

389   Probabilities: *P < 0.05; **P < 0.01; ***P < 0.001 and ns (not significant).

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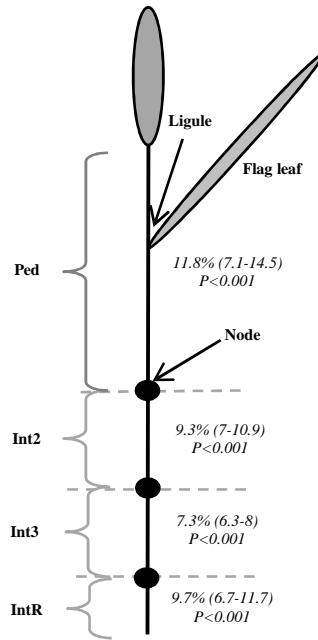
Figure 4. Diagram representing the stem internodes with mean values and ranges for internode dry matter as a proportion of shoot aboveground dry matter at GS65+7 days for the 26 CIMCOG cultivars. Values and ranges based on means in 2012 and 2013.

Stem-internode lengths were measured as proxies for stem-internode DM (Table 6). As expected, internode length decreased from the top to the base of the stem with the peduncle the longest internode in all cultivars (36.7 cm), followed by internode 2 (20.5 cm) (P <0.001). Internode 3 was slightly shorter than internode remainder (all internodes below internode 3) (P <0.001). In most cases, the IntR section was comprised of more than one basal internode. In contrast, internode specific weight (SW, mg cm^{-1}), or internode density (Table 6), increased from the top to the base of the stem, from 11.0 mg cm^{-1} in the peduncle to 22.3 mg cm^{-1} in the basal internodes (IntR).

Genetic variation was observed for all stem-internode traits (P< 0.05) apart from Int2 length and Int2 SW (Table 6). Strong associations between internode DM and their respective lengths were observed for all stem sections analysed, with the strongest linear relationships for Int2 (R^2 =0.76, P <0.001) and IntR (R^2 =0.71, P <0.001) (Fig. 5). Similarly, internode DM per shoot was strongly dependent on the specific weight in all stem sections, with the strongest correlations for internode 2 (R^2 =0.76, P <0.001) and the peduncle (R^2 =0.69, P <0.001) (Table 6).

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414 **Table 6.** Mean, maximum and minimum values for stem internode traits at GS65+7 days for the 26 CIMCOG
415 cultivars (Ped.: peduncle, Int2: internode 2 top-down (peduncle -1), Int3: internode 3 (peduncle -2) and IntR:
416 internode remainder (all internodes below internode 3) for the 26 CIMCOG cultivars and genetic correlations
417 with days from emergence to anthesis (DTA), stem-elongation period (days from initiation of booting to
418 anthesis, SEP), days from emergence to initiation of booting (DTInB), plant height (PH), grains m^{-2} (GN),
419 harvest index (HI), SPI: spike partitioning index (SPI) and Shoots m^{-2}: shoots per m^2 at GS65+7 days.
420 Correlations based on means on 2012 and 2013.

Trait	Dry-matter (mg shoot^{-1})				Length (cm)				Specific weight (mg cm^{-1})			
Phytomer	Ped	Int2	Int3	IntR	Ped	Int2	Int3	IntR	Ped	Int2	Int3	IntR
Overall mean	405	319	249	333	36.7	20.5	14.1	14.8	11.0	15.4	17.6	22.3
Overall maximum	538	394	299	474	44.2	23.3	16.5	19.5	13.2	18.0	21.0	27.6
Overall minimum	236	224	165	132	22.2	15.8	9.5	8.1	9.0	12.3	13.3	16.7
Mean 2012	414	284	231	305	36.4	19.8	14.1	14.2	11.3	14.3	16.3	21.2
Maximum 2012	540	380	299	450	44.4	23.8	16.3	19.0	14.2	17.3	20.1	29.2
Minimum 2012	242	139	131	95	21.4	13.7	10.4	6.0	9.1	11.4	12.9	15.5
Mean 2013	402	358	271	368	37.0	21.1	14.1	15.3	10.5	16.3	18.6	23.0
Maximum 2013	526	498	403	550	44.2	23.7	16.4	20.1	13.2	21.0	28.3	31.8
Minimum 2013	271	258	151	158	23.2	17.7	11.6	9.1	4.1	5.3	4.0	5.8
h^{2} [a]	0.85	0.65	0.76	0.58	0.91	0.92	0.79	0.68	0.83	0.24	0.63	0.67
CV [b]	16.8	18.4	13.0	20.4	7.6	3.7	4.8	13.2	12.1	17.1	12.7	13.7
LSD Gen. [c]	81.8	85.9	48.8	132	4.11	1.47	1.46	4.06	1.59	3.52	3.33	4.33
Prob. Gen.	***	***	***	**	***	Ns	***	***	***	ns	***	***
Prob. Year	ns	**	*	*	ns	**	ns	ns	ns	*	**	ns
Correl DTA	**-0.42**	-0.12	-0.11	0.29	**-0.61**	-0.29	**-0.43**	0.25	-0.08	0.08	0.22	0.15
Correl DTInB	**-0.54**	-0.20	-0.20	0.18	**-0.62**	-0.30	**-0.46**	0.22	-0.26	-0.04	0.12	0.01
Correl SEP	**0.48**	0.28	0.33	0.32	0.13	0.09	0.17	0.05	**0.62**	**0.40**	0.30	**0.48**
Correl PH	**0.70**	**0.80**	**0.65**	0.24	**0.78**	**0.87**	**0.77**	0.15	0.39	**0.53**	0.19	0.22
Correl Spikes m^{-2}	**-0.55**	**-0.67**	**-0.90**	**-0.86**	-0.25	-0.31	**-0.49**	-0.35	**-0.63**	**-0.99**	**-0.94**	**-0.98**
Correl GN	**-0.77**	**-0.73**	**-0.69**	-0.23	**-0.76**	**-0.69**	**-0.80**	0.05	**-0.50**	**-0.83**	-0.31	**-0.46**
Correl HI	-0.31	-0.02	0.13	0.18	-0.26	-0.17	-0.14	0.16	-0.23	0.21	0.21	0.13
Correl SPI	**-0.45**	**-0.56**	**-0.54**	-0.02	**-0.45**	**-0.56**	**-0.72**	0.02	-0.27	**-0.56**	-0.17	-0.16

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422 [a] broad sense heritability.

423 [b] *CV*.: coefficient of variation.
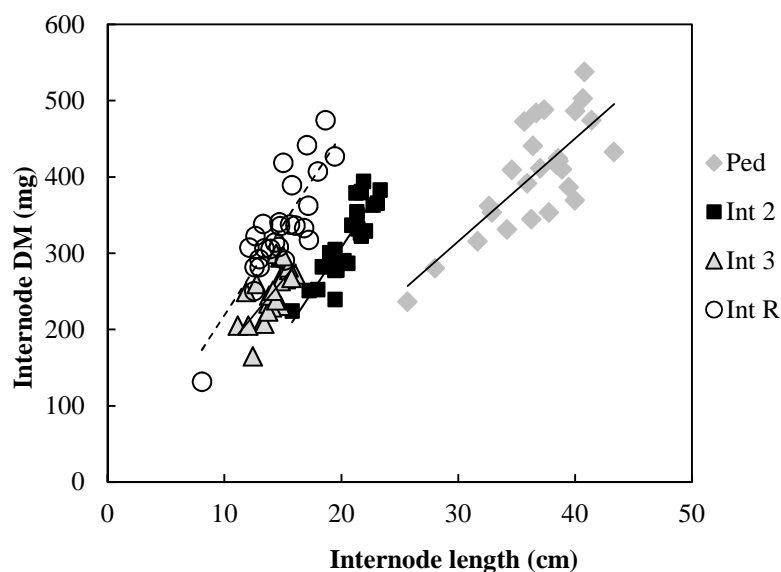
424 [c] *LSD* Gen.: Least significance difference (5%).

425 Probabilities: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ and ns (not significant).

426 For correlations, values in bold indicate significant correlation (at *$P < 0.05$ or lower).

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Figure 5. Linear regressions among the 26 CIMCOG cultivars for dry matter for each stem internode on their respective lengths Values represent means in 2012 and 2013.

Genetic correlations between internode morphological traits, phenological traits and plant height are shown in Table 6. Peduncle DM shoot[-1] was greater in cultivars with a longer stem-elongation period (DTInB to DTA; SEP). Phenology (DTInB, DTA or SEP) had no significant effect on DM shoot[-1] for the rest of the internodes (Table 6). A longer SEP had a positive effect on internode SW for Ped, Int2, and IntR. There were no significant effects of DTA or DTInB on internode SW. As expected, plant height was positively associated with internode DM shoot[-1] and length, with the exception of IntR; the strongest association was for Int2 DM shoot[-1] and length. However, plant height did not have a significant effect on SW in most internodes, showing only a significant correlation for Int2 SW (r=0.53, P <0.01) (Table 6).

DM and length were negatively correlated with SPI for most internodes, with the strongest associations for Int2 and Int3. IntR DM and length were not associated with SPI (Table 6). Regarding SW, most stem internodes were not associated with SPI, with the exception of Int3 that was strongly and negatively correlated with SPI (r =-0.56, P <0.01) (Table 6). Shoot density at GS65+7 days had a negative effect on DM shoot[-1] and SW for all internodes. Shoots m[-2] did not affect internode lengths apart from a small negative effect for Int3 (r =-0.49, P <0.05; Table 6). There were no significant correlations between shoots m[-2] and the proportion of DM partitioned to the stem internodes (correlations not shown).

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*3.3 DM partitioning traits at anthesis and spike growth and associations with harvest traits*

Averaging over years, there was no significant association between spike dry-matter (g m^{-2}) and stem DM (g m^{-2}) at GS65+7d (R^2 =0.11, P=0.1; Fig. 6a), suggesting a weak allometric relationship between the two organs. On the other hand, SDM was negatively associated with proportion of DM partitioned to the stem (R^2 =0.47, P <0.001; Fig. 6b). With respect to stem-internode DM partitioning, results showed that SDM (g m^{-2}) was negatively associated with the proportion of aboveground DM partitioned to Int2 (Int2 PI; R^2 =0.30, P <0.01) and Int3 (Int3 PI; R^2 =0.25, P <0.01) among the 26 cultivars (Fig. 7). No associations were observed between SDM and the Ped PI or IntR PI (Fig. 7).
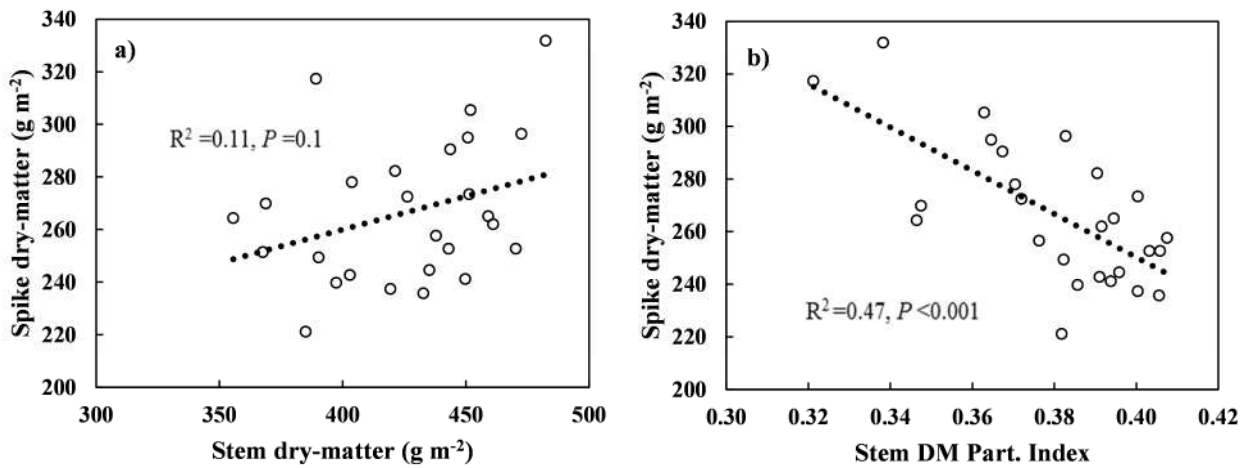
Figure 6. Linear regression of spike dry-matter (g m^{-2}) on a) Stem dry-matter (g m^{-2}) and b) Stem Partitioning indexer GS65+7 days for the 26 CIMCOG cultivars. Values represent means in 2012 and 2013.

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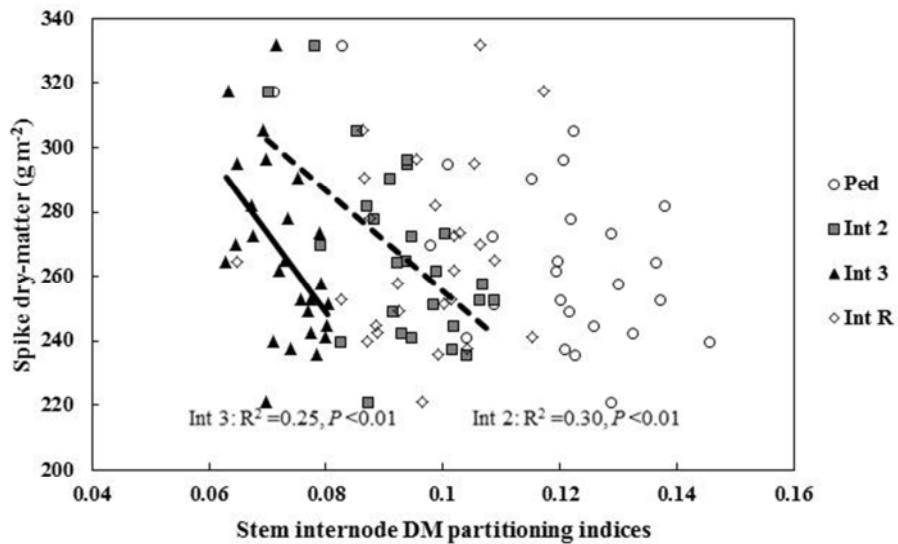
Figure 7. Linear regression of spike DM (g m^{-2}) on stem internode partitioning indices (stem internode DM as a proportion of aboveground DM) for the 26 CIMCOG cultivars.. Values represent means in 2012 and 2013.

Genetic correlations for DM partitioning traits at anthesis and harvest traits are shown in Table 4. Grains m^{-2} and grains per spike were strongly negatively associated with DM partitioning to the stem (r =-0.55, P <0.001 and r =-0.74, P <0.001; respectively). Dry-matter partitioning to the spike showed a positive association with GPS (r =0.52, P <0.01) but there was association with GN (r =0.31, ns). Thousand grain weight was strongly negatively correlated with SPI (r =-0.55, P <0.01) but positively with StPI (r =0.72, P <0.01), similar to the observed relationships between these DM partitioning indices and plant height. Stem internode DM and lengths were negatively and strongly associated with GN for most stem sections, with the exception of IntR (r= -0.23, r=0.05, ns, respectively) (Table 6). Thus, stem-internode DM and lengths were positively associated with increasing competition of spike growth and decreasing GN. There was generally a negative association between internode SW and GN, however, this was not significant for Int3 SW (Table 6). From the simple linear regressions, there were no significant correlations between HI and internode characteristics (DM PIs, lengths or SWs).

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485   When grouping cultivars in high and low biomass groups (13 cultivars each), it was clear that

486 high biomass cultivars relied more on higher SPI to increase HI (R^2 =0.50, P <0.01) compared to low

487 biomass cultivars (no association between SPI and HI) (Fig. S1a). Also, the observed trade-off

488 between SDM and StPI was stronger between the 13 cultivars with higher biomass expression (R^2

489 =0.63, P <0.01 vs R^2 =0.40, P <0.05, Fig. S1b).

490   A forward stepwise multiple linear regression with HI and SPI as dependent variables and

491 internode partitioning traits (DM PIs, lengths and DWs) and plant height and $AGDM_A$ as

492 independent variables was carried out (Table S1). Results showed that for SPI, as a single trait int3

493 length explained 23.1% of phenotypic variation and the regression model was not improved by the

494 addition of any further traits. For HI, as single trait plant height explained most phenotypic variation

495 (7.8%) and adding TSInt3PI (21.7%) to the regression model increased the variation accounted for

496 significantly. In summary, the proportion of DM partitioned to the spike at GS65+7 days was

497 positively correlated with HI, and traits related to GN such as SDM and GPS. In contrast, the

498 proportion of DM partitioned to the stems at GS65+7 days was negatively correlated with HI and

499 traits associated with GN determination (Table 4), such as SDM, GPS and FE. These trade-offs will

500 be addressed in the discussion section. Results from the multiple linear regression analysis showed

501 that stem int3 length was an important trait explaining variation for SPI, and that int3 stem PI

502 explained additional variation in HI compared to plant height alone.

503

504 *3.4 Genetic variation in non-grain spike dry-matter partitioning at harvest and associations with*

505 *fruiting efficiency*

506   Results from the cross-year analysis for non-grain spike DM partitioning at harvest are shown in

507 Table 6 for a subset of 17 cultivars, selected to represent the full range for FE with a restricted range

508 of anthesis date. The awns accounted for the highest proportion of non-grain spike DM (0.260; P

509 <0.001; Table 7: lemmas averaged 0.237 (P <0.001), glumes 0.204 (P <0.001), rachis 0.171 (P

510 <0.001) and paleas 0.127 (P <0.001). There was a year effect only for lemma DM partitioning (P

511 <0.05), but no significant year × cultivar interaction. Genetic correlation coefficients between FE_A,

512 FE_H, GPS and non-grain DM partitioning indices are presented in Table 7. Results indicated a

513 negative association between FE and rachis DM partitioning (r = -0.62, P <0.01 and r=-0.53, P

514 <0.05, respectively for FE_A and FE_H). On the other hand, FE was positively correlated with lemma

515 DM partitioning (r = 0.64 and r=0.61, P <0.01, respectively, for FE_A and FE_H). In addition, there

516 was a trend for a positive correlation between FE and palea DM partitioning (r = 0.43 and r=0.44, P

517 <0.1, respectively, for FE_A and FE_H). There was no significant correlation between awn DM

22

partitioning and FE. Rachis specific weight (RSW; mg cm^{-1}) was calculated for the subset 17
CIMCOG cultivars in 2013 and there were cultivar differences (P <0.001). Rachis SW showed a
strong negative correlation with FE$_H$ (r =-0.79 P <0.001) and a strong positive correlation with GPS
(r =0.71 P <0.01) (Table 6). The genetic correlation coefficient between FE$_A$ and RWS was close to
one (Table 7), due to a high phenotypic correlation coefficient between these traits (r_p=-0.61, P
<0.01; not shown) and a low heritability value for FE$_A$ in 2013 (h^2 =0.21; not shown).

Table 7. Non-grain spike DM partitioning at harvest and rachis specific weight (RSW) and genetic
correlations with fruiting efficiency calculated with chaff DM at harvest (FE$_H$), fruiting efficiency
calculated with spike DM at GS65+7 days (FE$_{A)}$ and grains per spike (GPS) for a subset of 17
CIMCOG cultivars . Values represent means of 2012 and 2013, except for RSW (2013).

Cultivar	[d] Proportion of spike					[e] RSW
	Rachis	Glume	Lemma	Palea	Awns	
1-BABAX/LR42	0.181	0.215	0.224	0.108	0.273	12.9
2-BACANORA T88	0.170	0.238	0.292	0.111	0.190	13.9
4-BECARD/KACHU	0.163	0.212	0.243	0.127	0.283	11.0
5-BRBT1*2/KIRITATI	0.177	0.185	0.243	0.123	0.273	13.6
7-SAUAL/WHEAR	0.184	0.214	0.242	0.130	0.231	14.7
8-CMH79A.955	0.178	0.209	0.223	0.121	0.271	15.1
14-PAVON F 76	0.159	0.180	0.244	0.137	0.280	11.4
15-PBW343*2	0.145	0.177	0.253	0.129	0.295	11.9
17-SERI M 82	0.162	0.194	0.231	0.139	0.274	12.6
18-SIETE CERROS T66	0.143	0.183	0.278	0.117	0.279	12.8
21-TACUPETO F2001	0.178	0.183	0.209	0.120	0.310	15.7
22-TC870344/GUI	0.166	0.183	0.236	0.124	0.291	13.1
23-TRAP#1/BOW	0.162	0.182	0.251	0.112	0.293	13.8
24-UP2338*2	0.171	0.211	0.266	0.134	0.217	13.6
25-BECARD	0.174	0.192	0.237	0.142	0.256	12.2
26-WBLL1*2/KURUKU*2	0.196	0.203	0.266	0.121	0.215	19.0
27-YAV_3/SCO//JO69	0.191	0.185	0.229	0.133	0.262	14.5
h^{2} [a]	0.93	0.87	0.85	0.41	0.93	0.90
CV [b]	5.4	7.8	8.1	15.2	7.9	7.5
LSD Gen. [c]	0.011	0.019	0.024	0.023	0.026	1.76
Prob. Gen.	***	***	***	0.061	***	***
Prob. Year	Ns	Ns	Ns	Ns	Ns	-
Prob. GenxY	Ns	Ns	Ns	Ns	Ns	-
Correl FE$_A$	**-0.62**	0.17	**0.64**	*0.43*	-0.33	§
Correl FE$_H$	**-0.53**	0.13	**0.61**	*0.44*	-0.28	**-0.79**
Correl GPS	0.24	0.20	-0.15	-0.28	-0.06	**0.71**

[a] broad sense heritability.

[b] *CV*.: coefficient of variation.

[c] *LSD* Gen.: Least significance difference (5%).

[d] Data from 2012 and 2013.

[e] Data from 2013.

534   §Genetic correlation was -1.0 due to high phenotypic correlation between these traits and low h^2 for FE_A in 2012 Probabilities:

535   *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ and ns (not significant). values in bold indicate significant correlation (at $P < 0.05$ or

536   lower).

537

4. Discussion

539   No systematic progress in harvest index in wheat has been shown in recent decades (Reynolds et

540 al. 2009) and several studies indicate that genetic increases in grain yield have been driven mostly by

541 increases in biomass in modern wheat cultivars (Shearman et al. 2005; Lopes et al. 2012b; Aisawi et

542 al. 2015). Indeed, the latest CIMMYT spring wheat releases expressed increased biomass as well as

543 grain yield, but decreased HI, precluding full expression of yield potential (Aisawi et al. 2015).

544 However, in order to translate improvements in biomass production into gains in yield potential, HI

545 must be maintained or ideally increased in high biomass cultivars (Reynolds et al. 2012). In this

546 context, this discussion will consider the scope to identify optimal dry-matter partitioning for

547 improved HI in elite wheat genotypes.

548

549 *4.1 Physiological mechanisms for achieving high grain yields in spring wheat*

550   Values of HI in the present study, and those reported elsewhere for winter (*ca.* 0.50-0.55) and

551 spring wheat (*ca.* 0.45-0.50) (Fischer 2007, 2011; Foulkes et al., 2011), are much less than the

552 theoretical limit for HI of *ca.* 0.62 (Austin 1980), indicating scope to raise HI in current CIMMYT

553 wheat cultivars and elsewhere. Grain yield in this study showed a linear association with $AGDM_H$

554 .consistent with recent studies showing positive associations between genetic yield progress and

555 biomass as well as radiation-use-efficiency (RUE)-related traits (Waddington et al. 1986; Donmez et

556 al. 2001; Shearman et al. 2005; Xiao et al. 2012; Beche et al. 2014; Aisawi et al. 2015). However, a

557 non-linear association between grain yield and HI for the 26 CIMCOG cultivars suggested

558 physiological barriers for biomass conversion to grain yield in high biomass cultivars. This could be

559 linked to non-optimal dry-matter partitioning, as the crop may allocate less biomass to agronomically

560 useful components associated with reproductive structures than is optimal (Slafer et al. 1999).

561   Plant height ranged from 0.81 to 1.16 m among the 26 cultivars, slightly higher than the optimal

562 range (0.7 to 1.0 m) for yield potential proposed by Miralles and Slafer (1995). Plant height was not

563 significantly associated with grain yield amongst the cultivars, although a trend for a positive

564 correlation with $AGDM_H$ was found ($r=0.35$, $P=0.10$). Some studies have reported positive

565 associations between plant height and crop biomass in modern cultivars (Slafer and Andrade 1989;

566 Calderini et al. 1995; Aisawi et al. 2015). The trend we observed for a positive association between

567 biomass and plant height could been linked to greater RUE associated with increased photosynthesis

24

568   due to a better light distribution in taller plants (Song et al. 2013). The raised-bed planting system in

569   the present study may also have contributed to the trend for taller plants, these cultivars achieving

570   earlier canopy closure in the gap between the beds (Fischer et al. 2005). However, taller plants in the

571   CIMGOG panel had lower GN, FE, SDM, SPI and also potentially lower HI (r= -0.37, P =0.10).

572   Thus, we hypothesise that small targeted reductions in plant height will not cause a negative impact

573   on yield and can be part of a strategy to favour spike growth and HI.

574   Overall, cultivar variation in HI was positively associated with both SPI (r = 0.46, P< 0.05) and

575   FE (r = 0.47, P> 0.05; FE_H) in the present study. However, variation in GN was better explained by

576   FE (r = 0.79, P< 0.001 for FE_A; and r = 0.95, P< 0.001 for FE_H) than SPI (r = 0.31, ns), although GN

577   was positively associated with SDM (r = 0.66, P< 0.01). Genetic variation in GN has been related to

578   SDM in wheat in many studies (Fischer, 1985, 2007; Fischer and Stockman, 1986; Slafer et al.,

579   1990; Miralles and Slafer, 2007; Reynolds et al., 2009). The non-significant association between SPI

580   and GN in the present study related mainly to a pair of cultivars (3-BCN/RIALTO and 22-

581   TC870344/GUI) with the highest expression of GN and average SPI, and when removing them from

582   the analysis there was a significant linear association between these traits (R^2 =0.24, P <0.05). Our

583   results indicated that reducing the length of internode 2 or 3 would be more effective in increasing

584   SPI and SDM (g m^{-2}) than reducing the length of the peduncle. This suggested there was greater

585   competition for assimilate between growing spikes and stem internodes 2 and 3 than the peduncle

586   during the critical floret survival phase between booting and anthesis (Brooking and Kirby 1981;

587   Fischer and Stockman 1986a).

588   The complementary trait to SPI to increase GN and HI is the fruiting efficiency which is

589   potentially additive to SPI (Foulkes et al. 2011; Lázaro and Abbate 2011; Slafer et al. 2015). In the

590   present study, values of FE_A were lower than those for FE_H, although both showed high genetic

591   variation among the 26 CIMCOG cultivars. Various studies have reported genetic variation for FE

592   and associations with grains m^{-2} across a wide range of environments (Abbate et al. 1998; Gaju et al.

593   2009, 2014; González et al. 2011; Lázaro and Abbate 2011; Bustos et al. 2013; Aisawi et al. 2015).

594   Absolute values of FE depend partly on the method of calculation, but FE calculated with spike DM

595   at anthesis shows high correlation with FE calculated with chaff DM at harvest (Abbate et al. 2013).

596   Our results also showed a good correlation between FE_A and FE_H (r = 0.77, P < 0.001). Fruiting

597   efficiency in spring wheat ranged from 42 to 91 grains g^{-1} based on SDM one week after anthesis

598   (Gaju et al. 2014; García et al. 2014) and from 35 to 137 grains g^{-1} based on chaff DM at harvest

599   (González et al., 2011; Abbate et al., 2013). In the present study, values for FE_H were overall 35%

600   higher than those for FE_A. In contrast, Abbate et al. (2013) observed in Argentinian bread-wheat

25

601 cultivars FE at harvest was 8% lower than FE at anthesis. Furthermore, chaff dry weight at harvest is

602 reported to be 20-50% higher than spike DM at anthesis (Stockman et al. 1983; Fischer 2011; Abbate

603 et al. 2013). Analysis of grain dry weight at GS65+7d among six CIMCOG cultivars in 2013 showed

604 developing grains represented from 12.2 to 22.2% of spike dry weight (data not shown). These

605 developing grains in the spike could partly explain lower FE_A values compared to FE_H in our study.

606 Further work is needed to explore the reasons behind these differences, also taking into account

607 retranslocation of water soluble carbohydrates.

608   Encouragingly trade-offs between FE and SDM or SPI at GS65+7d were not observed among

609 CIMCOG cultivars, indicating a degree of independence between these traits. As SDM is one of the

610 two numerical components of FE, one avenue to increase FE could be decreasing SDM. However,

611 reducing SDM is likely to have negative effects on the amount of assimilate available during floret

612 survival. Some previous studies showed evidence for trade-offs between SDM and FE in bread

613 wheat cultivars and/or advanced lines (Gaju et al. 2009; Lázaro and Abbate 2011). However,

614 González et al. (2011) found that GN was highly associated with both FE and SDM and Abbate et al.

615 (1998) reported differences in FE for comparable SDM values. Therefore, our results and previous

616 evidence suggest that it is possible to increase SDM and SPI without having negative effects on FE.

617 Our results showed a negative association between TGW and FE, although compensation was not

618 complete and there were still gains in GN, HI and grain yield with increasing FE. Slafer et al. (2015)

619 suggested that a trade-off between FE and TGW may be linked to the production of smaller florets

620 with lower grain weight potential and that to break the trade-off increases in FE could be targeted

621 independent of the size of the florets.

622

623 *4.2 Optimal DM partitioning at anthesis for grain number and HI*

624   Although genetic variation in SDM has been generally more associated with SPI than

625 aboveground dry-matter at anthesis (Slafer et al., 1990), variation in SDM in the CIMCOG panel was

626 associated more strongly with $AGDM_{A7}$ (r =0.91, *P* <0.001) than SPI (r =0.43, *P* <0.05). Spike

627 partitioning index was reported to range from 0.12 to 0.21 for winter wheat cultivars in the UK

628 (Shearman et al. 2005) and from 0.16 to 0.29 for spring wheat genotypes in Australia and Mexico

629 (Siddique et al. 1989; Reynolds et al. 2001; Gaju 2007). In the present study, SPI ranged from 0.21

630 to 0.26 among the 26 CIMCOG cultivars, showing values slightly lower than the maximum reported

631 previously for spring wheat. Increases in SPI through breeding have been strongly linked to HI

632 (Slafer et al. 2005). Slafer et al. (1990) found a significant positive trend between SPI and the year of

633 release (YoR) in six Argentinian bread-wheat cultivars released between 1912 and 1980. However, a

recent study on CIMMYT spring wheat cultivars reported decreases in SPI over a 43-year period from 0.25 to 0.23, SPI decreasing from about *ca.* 1980 (Aisawi et al. 2015), matching the changes in HI over the same period of time. Similar results for SPI were found in the present study in the subset of eight CIMCOG historic cultivars, where SPI decreased from 0.50 to 0.47 from 1982 to 2005 . Decreases in SPI with breeding could be associated with increases in plant height within CIMMYT semi-dwarf cultivars (Aisawi et al. 2015). The maximum StPI was greater among the 26 CIMCOG cultivars (genetic range 0.48 to 0.65) than that reported previously for CIMMYT cultivars. Aisawi et al. (2015) observed StPI to range from 0.52 to 0.57, and to increase from 0.53 to 0.56 over the 43-year period from 1966 to 2009, associated with increases in plant height from 94 to 105 cm. Finally, present results for genetic variation in lamina partitioning index (0.16 – 0.22) were similar to values reported in the UK for winter wheat (0.19 – 0.21) (Shearman, 2001), but lower than values previously reported for spring wheat in Mexico (0.25 – 0.31) (Gaju 2007).

Assimilates partitioned to the spike determine the proportion of floret primordia as competent florets at anthesis (Fischer 1985). Among the 26 CIMCOG cultivars, there was a negative association between SDM and StPI (R^2 =0.47, *P* <0.001), and also between SPI and StPI (*r* =-0.61, *P* <0.05), since timing for rapid growth of stem (stem elongation) and spike coincide (Kirby 1988). We hypothesised that competition for assimilates between stems and spikes differs according to the internode position, related to the extent of overlap between the extension of upper internodes and the rapid spike growth phase (Borrell et al. 1993). Present results for the 26 cultivars showed that stem DM partitioning to Int2 (Int2 PI) and Int3 (Int3 PI) was negatively associated with SPI and SDM. Although it has been suggested that reductions in peduncle length may favour spike partitioning, as this organ extends most rapidly before anthesis (Richards 1996), present results may reflect that the peduncle is still elongating and accumulating structural DM after anthesis. Therefore, peduncle stem growth may coincide less with the window for floret mortality during the rapid spike growth phase before anthesis than that of Int2 and Int3.

Since stem Int2 PI and Int3 PI are difficult to measure in breeders' plots, it is important to identify other morphological attributes indicative of stem DM partitioning in these internodes that breeders could select for to enhance SPI, SDM and HI. In this respect, present results showed that stem internode length is highly associated with internode DM shoot^{-1}. Reducing DM to internode 2 and 3 to increase SDM could be aligned with changes in basal internode morphology to maintain minimum requirements for a lodging-proof plant (Piñera-Chavez et al. 2016). In our results, as a single trait stem-internode traits did not correlate significantly with HI. However, a forward stepwise multiple linear regression applied to cross-year genotype means with HI as the dependent variable

667 testing stem-internode traits, plant height and $AGDM_{A7}$ as independent variables showed that plant

668 height explained most phenotypic variation (7.8%) in HI as a single trait but adding the stem Int3 PI

669 (21.7%) improved regression model significantly.

670 *4.4 Avenues to increase FE using dry-matter partitioning traits*

671   Present results showed a negative association between the FE and rachis DM partitioning and a

672 positive association with lemma DM partitioning (as a proportion of non-grain spike DM). In

673 addition, there was a negative association between FE and rachis specific weight (RSW). Abbate et

674 al. (1998) reported differences in the proportion of rachis in spike DM in six varieties of semi-dwarf

675 awned spring wheat, and hypothesized that higher FE could be achieved through a lower allocation

676 of spike DM to non-productive sinks (glumes, awns and rachis). Gaju et al. (2009) found a positive

677 association between FE and rachis length per spikelet in CIMMYT spring wheat genotypes,

678 hypothesising a longer rachis per spikelet favoured spikelet photosynthesis and higher assimilate

679 supply to florets. It has been reported that floret survival is positively associated with sugar content

680 of the spike (Ghiglione et al. 2008; Dreccer et al. 2014), suggesting that high soluble carbohydrate

681 content in spikes might be associated with increased FE. Alternatively, FE in wheat may be related to

682 modifying plant signalling responses (González et al. 2011; Gonzalez-Navarro et al. 2016). Elevated

683 cytokinin concentration in panicles related to regulation of cytokinin oxidase were shown to increase

684 grain number in rice (Ashikari et al. 2005). Overall our results suggested that a decreased relative

685 DM partitioning to the rachis and increase relative partitioning to the lemma within the spikelet

686 morphological components could favour increased FE.

687

688 **5 Conclusions**

689 The present study indicated that Int2 and Int3 length accounted for 26% and 27% variation in SPI,

690 respectively, and rachis PI, lemma PI and rachis SW accounted for 24%, 23% and 25% variation in

691 fruiting efficiency, respectively. It is suggested that screens for these traits may have value in plant

692 breeding programs aimed at improving GN and HI in high biomass backgrounds. High-throughput

693 assessment methods would be required for the deployment of these traits in plant breeding programs.

694 Internode 2 and 3 length can be scored at moderately high throughput; in our study we assessed

695 internode lengths on 10 shoots per plot for 26 genotypes in three replicates (78 plots) in

696 approximately three person-hours. It is likely the sample size could be reduced to 7 shoots per plot

697 with relatively little reduction in precision (Pinera-Chavez, 2016). However, for rachis and lemma PI

698 and RSW current phenotyping methods are time consuming and no high-throughput field screens are

699 presently available. In these cases, the implementation of QTL for selection of these traits can

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potentially counteract this shortcoming of labour intensive phenotyping. Therefore, the genetic basis of these traits must be established for deployment in marker-assisted selection in breeding. Genetic analysis of these traits is ongoing by the authors through a GWAS study on a CIMMYT spring wheat high biomass association panel (HiBAP) (Sierra-Gonzalez *et al*., 2019). The deployment of these traits in wheat breeding will also depend on heritability (Sadras and Rebetzke 2013; Cooper and Bänziger 2017). In this study, the grain partitioning traits (internode lengths, SPI, FE, rachis and lemma PI and RSW) had heritability > 60%, and therefore have scope for application in breeding (Lopes et al. 2012a; Sukumaran et al. 2017). Further work will be needed to understand and account for any trade-offs between changes in internode lengths and soluble carbohydrate accumulation and lodging resistance and to understand better the degree to which the apparent trade-offs may be genetically dependent.

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939 **Supplementary material**

940   **Table S1**. Stepwise multiple linear regression analysis with harvest index (HI) and
941   spike partitioning index (SPI) as dependent variables for 26 CIMCOG genotypes.
942   Independent variables selected in the analyses contributed significantly to the models.
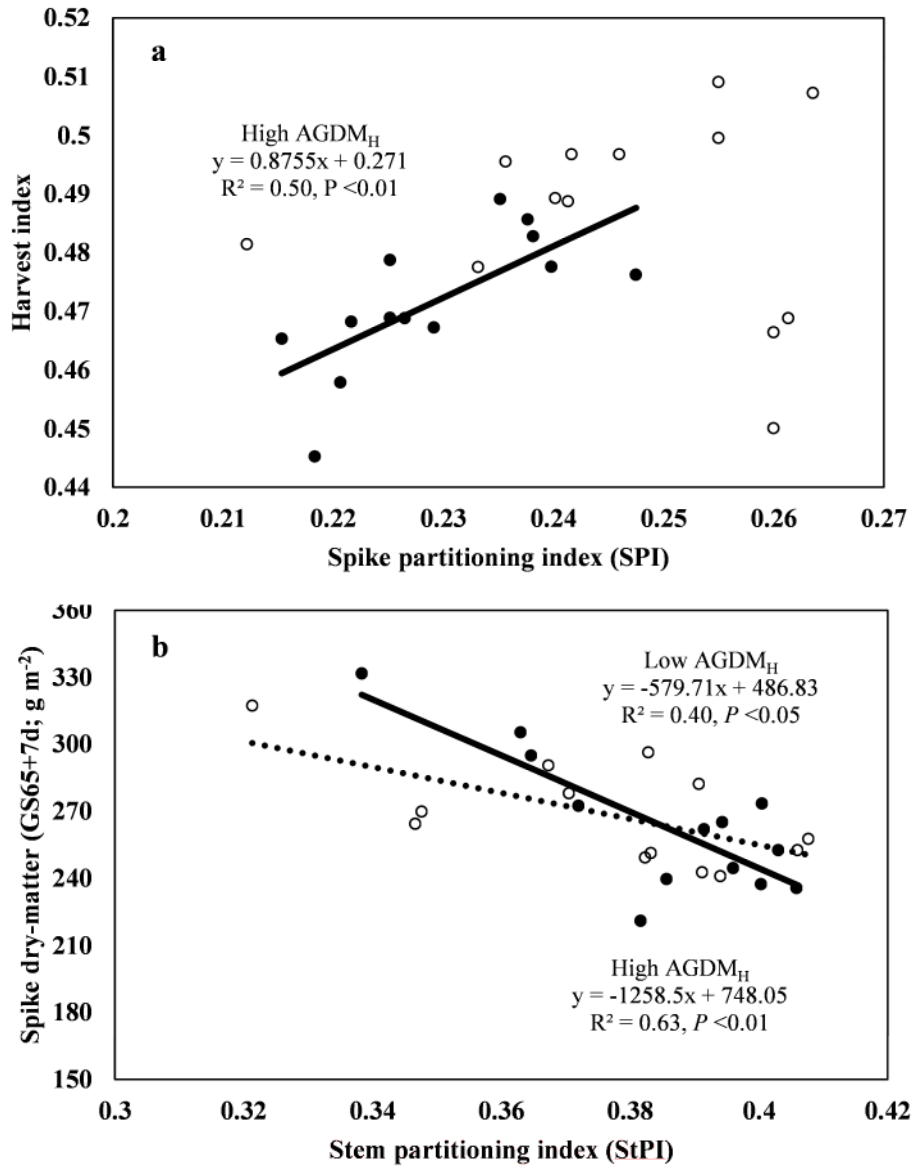
943

Traits	Variable selected	R^2	Sig.	Variables tested in model
HI	Plant height	7.8	0.049	Plant height, Ped length, Int2 length, Int3
	Int3 PI	21.7	0.021	length, Ped PI, Int2 PI, Int3 PI, Ped SW, Int2
				SW, Int 3 SW, $AGDM_{A7}$.
SPI	Int 3 length	23.06	0.007	Plant height, Ped length, Int2 length, Int3
				length, Ped PI, Int2 PI, Int3 PI, Ped SW Int2
				SW, Int 3 SW, $AGDM_{A7}$.

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Figure S1. Linear regression of a) Harvest index on stem DM partitioning index (stem DM/aboveground DM) and b) spike DM at GS65+7 days (SDM, g m^{-2}) on stem DM partitioning index (stem DM/aboveground DM). Closed symbols represent a 13 cultivars subset with the highest expression of AGDM$_H$ and open symbols represent a 13 cultivars subset with the lowest expression of AGDM$_H$.

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