

1 **Optimizing dry-matter partitioning for increased spike growth, grain number**
2 **and harvest index in spring wheat**

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18

19 **Abstract**

20 Improving biomass is an important goal for future genetic gains in yield potential in wheat, but it will
21 also be crucial to identify physiological traits to maximize harvest index (HI, proportion of
22 aboveground biomass in grain). Increased grain partitioning will require increased dry-matter (DM)
23 partitioning to the spikes at anthesis as well as enhanced fruiting efficiency (FE, grains per g spike
24 dry matter at anthesis or chaff dry matter at harvest), whilst optimizing the partitioning amongst the
25 non-grain components to maintain post-anthesis photosynthetic capacity and soluble carbohydrate
26 translocation. The objectives of this study were to: i) quantify genetic variation in DM partitioning
27 among plant organs at anthesis (GS65) + 7days and associations with spike growth and FE and ii)
28 identify optimized partitioning traits associated with enhanced HI and grain yield, in CIMMYT elite
29 spring wheat backgrounds. Two field experiments were conducted in 2011-12 and 2012-13 testing
30 26 CIMMYT spring wheat cultivars in NW Mexico in irrigated conditions in which DM partitioning
31 was assessed in plant organs at anthesis + 7 days, and within-spike (glume, palea, lemma, rachis and
32 awn) partitioning was assessed at harvest. Grain yield, yield components, HI and FE were assessed at
33 harvest. Our results identified new traits for HI (decreased DM partitioning to stem internodes 2 (top
34 down, peduncle -1) and 3, and decreased rachis DM partitioning and rachis specific weight (rachis
35 DM per rachis unit length) and increased lemma DM partitioning), potentially allowing breeders to
36 maximize the exploitation of enhanced carbon assimilation for grain biomass. Further work will
37 focus on understanding the role of soluble carbohydrate re-translocation in these relationships and
38 establishing high-throughput and cost-effective phenotyping methods for these traits for deployment
39 in breeding.

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46 *Abbreviations:* FE, Fruiting efficiency; SPI, Spike partitioning index; StPI, Stem partitioning
47 index; LPI, Lamina partitioning index; LSPI, Leaf sheath partitioning index; Ped, Peduncle;
48 Int2, Internode 2; Int3, Internode 3; IntR, Internode remainder; DTA, Days emergence to
49 anthesis; GPSGrains per spike; SDM, Spike dry-matter; SPN, Spikes m⁻²; DTInB, Days from
50 emergence to initiation of booting; SEP, Stem elongation period (days from initiation of booting to
51 anthesis).

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53 1. Introduction

54 Wheat (*Triticum aestivum* L.) is globally grown on more than 220 million hectares of land with a
55 global average yield of 3.41 t ha⁻¹ (FAO 2006). Annual genetic gains for grain yield of wheat in
56 CIMMYT international Elite Spring Wheat Yield Trials from 2007 to 2015 were 0.53% in optimally
57 irrigated environments compared to local checks (Crespo-Herrera et al. 2017). The current annual
58 rate of genetic gain in wheat yield potential from datasets reported globally averages 0.6% (0.3% -
59 1.1%) (Fischer et al. 2014). However, the rates of yield gains required to meet predicted global
60 demand for cereals in 2050 are higher than the present rates of genetic gains at ca. 1.16% - 1.31% per
61 annum (Hall and Richards 2013). Studies on historic sets of cultivars have shown yield progress has
62 been associated with greater above-ground biomass in the UK (Shearman et al. 2005), Australia
63 (Sadras and Lawson 2011), China (Xiao et al. 2012), Brazil (Beche et al. 2014) and NW Mexico
64 (Aisawi et al. 2015). Some of these studies have shown yield progress was also associated with HI
65 (Xiao et al. 2012; Beche et al. 2014) while others report no systematic progress in HI in the last
66 decades (Shearman et al. 2005; Aisawi et al. 2015). For example, HI has actually decreased in
67 CIMMYT spring wheat cultivars in NW Mexico from 1990 to 2009 (Aisawi et al. 2015). In contrast,
68 in Argentinian wheat cultivars released from 1999-2011 yield progress of 0.18% year⁻¹ was
69 associated with an increase in HI of 0.25% year⁻¹ with no association with overall above-ground
70 biomass (Lo Valvo et al. 2018). Overall this evidence, combined with the reported co-limitation of
71 grain growth by source and sink during grain filling in modern wheat varieties (Shearman et al.
72 2005; Acreche and Slafer 2009; Aisawi et al. 2015), indicates that simultaneous increase of
73 photosynthetic capacity and grain partitioning in modern wheat cultivars is a crucial task for
74 breeders. To exploit future genetic gains in biomass for yield potential, it will be necessary to
75 identify traits enabling breeders to discriminate 'useful' and 'non useful' biomass in new high
76 biomass cultivars to maximize partitioning to grain and yield potential gains.

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

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

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

96 Since stem and spike growth overlaps during stem elongation mainly during the rapid spike
97 growth phase from booting to anthesis (Brooking and Kirby 1981), the extent of competition
98 between the spike and stem should differ between stem internodes. The timing of maximum stem
99 growth rates has been reported to vary from 11-17 days before anthesis to around anthesis (Borrell et
100 al. 1989, 1991; Youssefian et al. 1992), i.e., when both the peduncle and the penultimate internode
101 are rapidly extending (Youssefian et al. 1992). However, maximum stem length is usually reached
102 after anthesis (Borrell et al. 1989; Youssefian et al. 1992; Bonnett and Incoll 1992; Ehdaie et al.
103 2006), with post-anthesis stem extension attributed solely to peduncle extension. Genetic variation in
104 stem-internode partitioning has been reported in association with stem dry-matter loss and grain
105 growth (Borrell et al. 1993; Ehdaie et al. 2006) in studies comparing tall versus semi-dwarf cultivars,
106 but to our knowledge not previously in elite semi-dwarf cultivars directly related to pre-anthesis
107 spike growth.

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

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

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

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137 **2. Materials and Methods**

138 *2.1. Plant material and experimental conditions and design*

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

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

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

168 Season and long-term data for daily mean air temperature, daily mean solar radiation and
169 accumulated monthly rainfall were collected from a weather station located 1-2 km from the field
170 experiments (Table 2). Mean air temperature during December (~GS10-GS29) was $2.7 \text{ }^{\circ}\text{C}$ colder in
171 2012 compared to 2013. During January, February and March (GS31-early grain filling), mean air
172 temperature was $1.7 \text{ }^{\circ}\text{C}$ colder in 2012 than in 2013. Mean air temperature during most of late grain
173 filling was similar in both years, but slightly warmer in 2012 ($+0.6 \text{ }^{\circ}\text{C}$). Mean solar radiation was
174 similar in both seasons for most months, with the exception of April, having $3.5 \text{ MJ m}^{-2} \text{ day}^{-1}$ more
175 in 2012 than in 2013. Accumulated rainfall was similar during pre-anthesis (December-February)
176 and grain filling (March-April) in both seasons.

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185 **Table 1.** Code number, year of release (YoR) and cultivar name for the 26 cultivars in the CIMCOG panel in
 186 2012 and 2013 at Cd. Obregon. NW Mexico. Historic cultivars are shaded. Cultivars in bold represent the
 187 selection for the non-grain spike dry-matter partitioning analysis. Reduced height *Rht-B1a/Rht-B1b*, *Rht-*
 188 *D1a/Rht-D1b*, and photoperiod insensitivity *Ppd-D1a/Ppd-D1b* classes, and average days to anthesis (DTA;
 189 days after emergence, DAE) and plant height (PH) of 26 CIMCOG cultivars. Values represent means in 2012
 190 and 2013. The *Rht-B1b* and *Rht-D1b* alleles confer semi-dwarf stature and the *Ppd-D1a* allele confers
 191 insensitivity to photoperiod.

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

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193 **Table 2.** Environmental conditions at the experimental site for each field season (2012 and 2013) during the wheat cycle
 194 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

195 2.3. *Crop measurements*

196 Unless otherwise stated, measurements were carried out in all 26 cultivars. In each experiment,
197 plants were counted in each plot shortly after emergence in a 0.8 m² area. Dates of initiation of
198 booting (GS41), onset of anthesis (GS65) (Zadoks et al. 1974) and physiological maturity (GS89)
199 (50% of the peduncle with a yellow colouration) were recorded for each plot, when 50% of the
200 shoots in the plot were at the stage. Plant height to the tip of the spike was recorded at four positions
201 in each plot shortly before physiological maturity. In both years, in each plot plant material was
202 sampled at anthesis +7 days (GS65+7) (samples taken on actual date of reaching the stage) in an area
203 of 0.8 m² (four 50 cm length rows, 1.6 m total width) by cutting at ground level. A sub-sample
204 consisting of 100 shoots was taken and the weight recorded before and after oven drying at 70°C for
205 48 h to constant weight. Before oven drying, infertile shoots (those without an emerged spike) were
206 counted in the sub-sample; the remaining shoots were classified as fertile. From the remaining
207 sample, ten randomly selected fertile shoots were separated into: i) leaf lamina ii) leaf sheath, iii)
208 stem and iv) spike. The weight of each plant component was recorded after drying at 70°C for 48 h
209 to constant weight. The DM partitioning indices of each component (lamina partitioning index, LPI;
210 leaf sheath partitioning index, ShPI; stem partitioning index, StPI and spike partitioning index, SPI)
211 were calculated as the ratio of plant component DM/aboveground DM. In addition, the ten stems (iii)
212 were further separated into their phytomers, peduncle (Ped), internode 2 (Int2), internode 3 (Int3)
213 and internode remainder (IntR). Internode lengths were recorded. After oven drying at 70°C for 48 h
214 to constant weight, dry weights were recorded separately for each internode. The DM partitioning
215 indices of each internode were calculated as the ratio of internode DM/aboveground DM (peduncle
216 DM partitioning index, Ped PI; internode 2 DM partitioning index, Int2 PI; internode 2 DM
217 partitioning index, Int3 PI and internode remainder DM partitioning index, IntR PI). Internode
218 specific weight (SW) was calculated by dividing the internode DM shoot⁻¹ by the internode length
219 (cm) and is expressed as mg cm⁻¹ for each internode (Ped SW, Int2 SW, Int3 SW and IntR
220 SW). Fruiting efficiency was calculated based on the spike DM per m² at GS65+7 days (FE_A) and
221 also based on the chaff DM per m² at harvest (non-grain spike DM) (FE_H), by dividing the grains m⁻²
222 at harvest by the spike or chaff DM (g m⁻²). After physiological maturity, grain yield was measured
223 in each plot by machine-harvesting an average plot area of 5.7 m² and 4.8 m² in 2012 and 2013,
224 respectively, and values adjusted to 15% moisture. Prior to that, a random sample of 100 fertile
225 shoots was taken at physiological maturity, cutting shoots at ground level. The plant material was
226 oven dried for 48 h at 70°C to constant weight, weighed, then threshed and the grain collected and
227 weighed. From this lot, 200 grains were randomly counted and weighed. Using these data, harvest

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).

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{re}} \quad (1)$$

251
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):

$$r_g = \frac{\overline{\sigma_{g(jj')}}}{\overline{\sigma_{g(j)}\sigma_{g(j')}}} \quad (2)$$

258

259 where $\overline{\sigma_{g(jj')}}$ is the adjusted mean of all pairwise genotypic covariances between trait j and j' and
 260 $\overline{\sigma_{g(j)}\sigma_{g(j')}}$ 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 $\text{square}/\text{total mean square}))$.

268

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

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).

295

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 $g m^{-2}$	TGW g	HI .	$AGDM_H$ $g m^{-2}$	GN m^{-2}	SPN m^{-2}	GPS	DTA Days	DTM Days	PH cm	$Chaff_H$ $g m^{-2}$	FE_A grain	FE_H 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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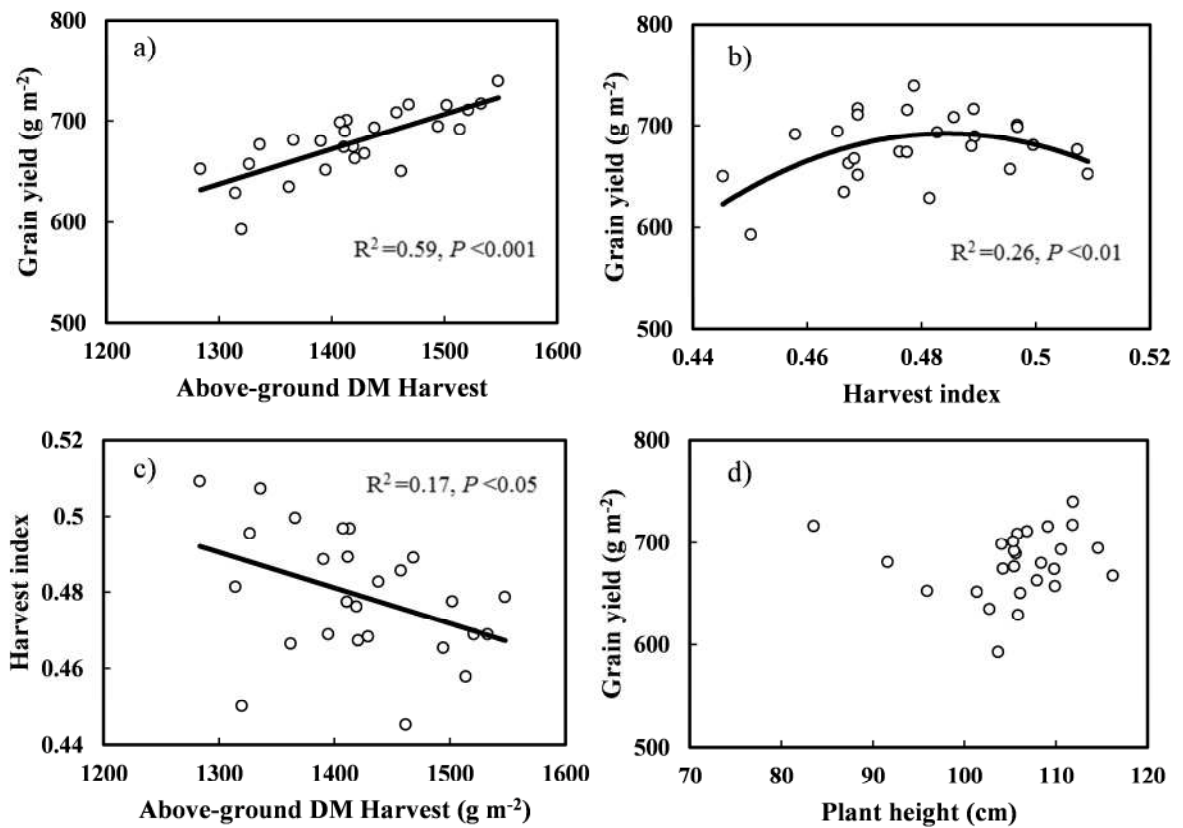
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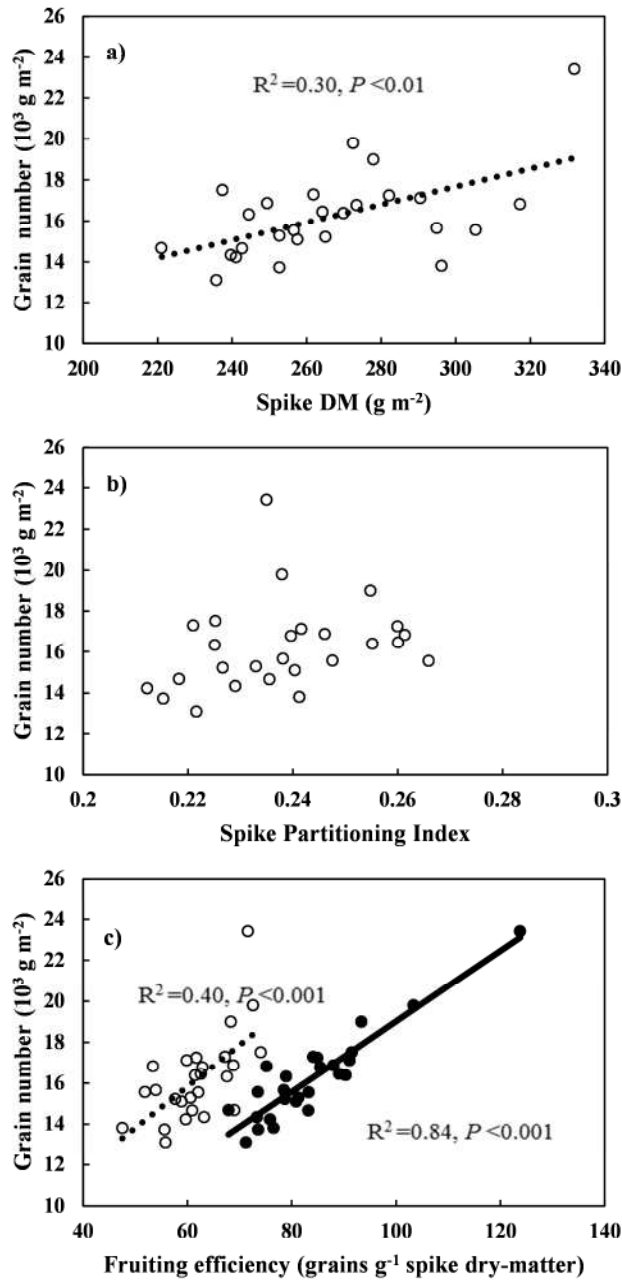
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Figure 1. Regression among the 26 CIMCOG cultivars of a) grain yield (100% DM) on above-ground dry-matter (AGDM) at harvest, b) grain yield on harvest index, c) harvest index on AGDM at harvest and d) grain yield on plant height. Values represent means in 2012 and 2013.

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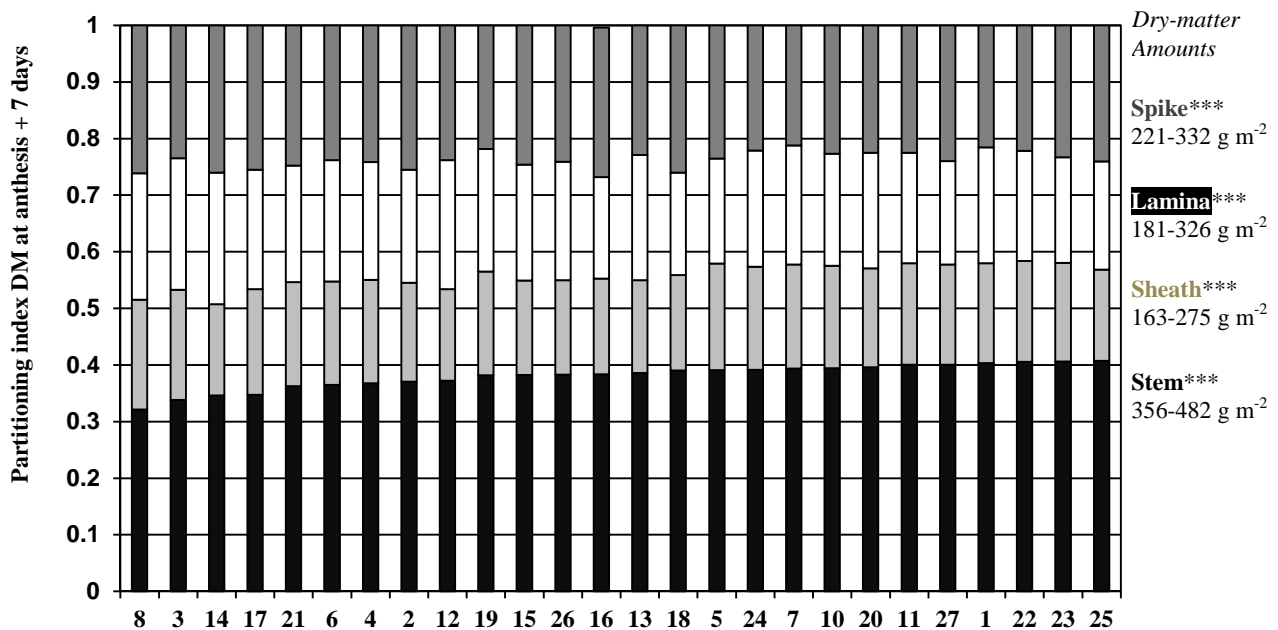


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Figure 2. Linear regressions among the 26 CIMCOG cultivars for grains m^{-2} (GN) on a) spike dry-matter (g m^{-2}) at GS65 + 7days, b) spike partitioning index and c) fruiting efficiency (grains per gram of spike dry-matter m^{-2}). In c), open symbols 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.

331 3.2. Genetic variation in dry-matter partitioning at anthesis

332 The aboveground DM at GS65+7d differed among the 26 cultivars (Table 5), and showed no
 333 significant correlation with AGDM_H ($r = -0.36$, $P > 0.1$; Table 4). Spike DM at GS65+7d (SDM)
 334 ranged from 226 to 314 g m⁻² ($P < 0.001$) (Table 5). Although there was variation for spike number
 335 m⁻² at GS65+7d (236 - 401, $P < 0.001$; Table 3), differences in SDM (g m⁻²) were associated with
 336 spike DM per shoot ($R^2 = 0.46$, $P < 0.05$) rather than spikes per m² (ns). There were significant
 337 differences among cultivars in the DM partitioning to the spikes, stems, leaf laminae and leaf
 338 sheaths. Averaged across years, spike partitioning index ranged from 0.21 to 0.26 ($P < 0.001$, Table
 339 5, Fig. 3) and the stem DM partitioning index from 0.32 to 0.41 amongst the 26 cultivars ($P < 0.001$,
 340 Fig. 3). Lamina DM partitioning index and leaf-sheath DM partitioning index showed similar values,
 341 with ranges of 0.18-0.23 and 0.16-0.20 ($P < 0.001$), respectively (Fig. 3). Dry-matter amounts for the
 342 different plant components (Fig. 3) ranged from 356-482 g m⁻² for stems, 221-332 g m⁻² for spikes,
 343 181-326 g m⁻² for the laminae and 163-275 g m⁻² for leaf sheaths ($P < 0.001$) amongst the 26
 344 cultivars.



345 **Figure 3.** Dry-matter partitioning indices and dry-matter amounts for each plant component for the 26
 346 CIMCOG cultivars at GS65+7d. Values represent means in 2012 and 2013.

347 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
 348 =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).

349 h^2 : broad sense heritability.

350 LSD: Least significance difference (5%);

351 Prob. Gen: Probability for genotype.

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

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356 **Table 4.** Genetic correlations between dry-matter (DM) partitioning related traits at GS65+7 days and key
 357 harvest traits among the 26 CIMCOG cultivars (based on cross-year means in 2012 and 2013). GY: grain
 358 yield, TGW: thousand grain weight, HI: harvest index (HI), AGDM_H: aboveground DM at harvest, GN: grains
 359 m⁻², SPN: spikes m⁻², GPS: grains per spike, DTA: days from emergence to anthesis, DTM: days from
 360 emergence to maturity, PH: plant height (PH), FE_H: fruiting efficiency calculated with chaff DM at harvest,
 361 FE_A: fruiting efficiency calculated with spike DM at GS65+7 days, AGDM_{A7}: aboveground DM at GS65+7
 362 days, SDM: spike DM at GS65+7 days, SPI: spike partitioning index, StPI: stem partitioning index, LPI:
 363 lamina partitioning index and ShPI: sheath partitioning index. Values in bold indicate significant correlation
 364 (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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367 Plant height was negatively correlated with AGDM_{A7} ($r = -0.54$, $P < 0.01$) and with SPI ($r = -0.48$,
 368 $P < 0.05$) and positively with StPI ($r = 0.71$, $P < 0.001$) (Table 4). Moreover, a later DTA had a
 369 negative effect on StPI, a positive effect on LPI and ShPI and no effect on SPI (Table 4). There was
 370 no effect of spikes m⁻² on AGDM_{A7} or on the DM partitioning indices or amounts in the spike, stem,
 371 leaf sheaths or lamina (Table 4).

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

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 ($P < 0.001$).

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Table 5. Mean, maximum and minimum values for aboveground dry-matter ($AGDM_{A7}$), spikes per m^2 , spike partitioning index (SPI) and spike DM per m^2 (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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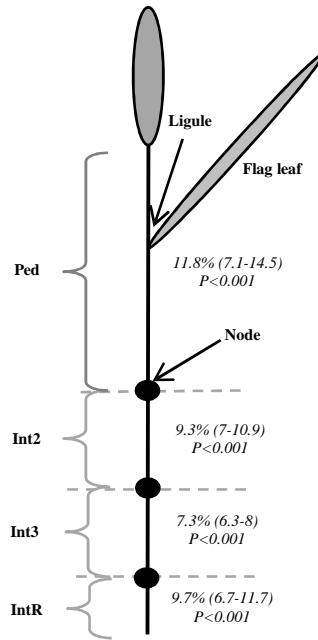
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^a broad sense heritability.

^b CV : coefficient of variation.

^c LSD Gen.: Least significance difference (5%).

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).

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 m² 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)			
	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
<i>h</i> 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
<i>CV</i> ^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

421 ^a broad sense heritability.

422 ^b *CV*.: coefficient of variation.

423 ^c *LSD* Gen.: Least significance difference (5%).

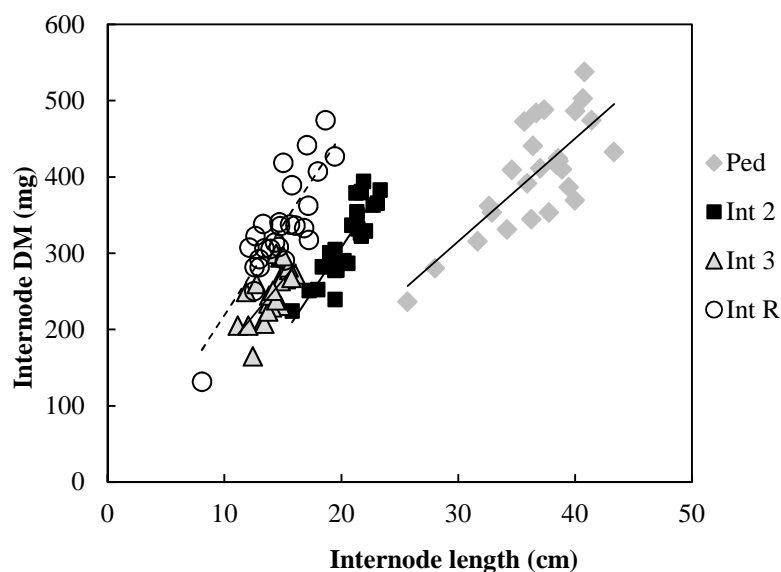
424 Probabilities: **P* < 0.05; ***P* < 0.01; ****P* < 0.001 and ns (not significant).

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

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

432

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

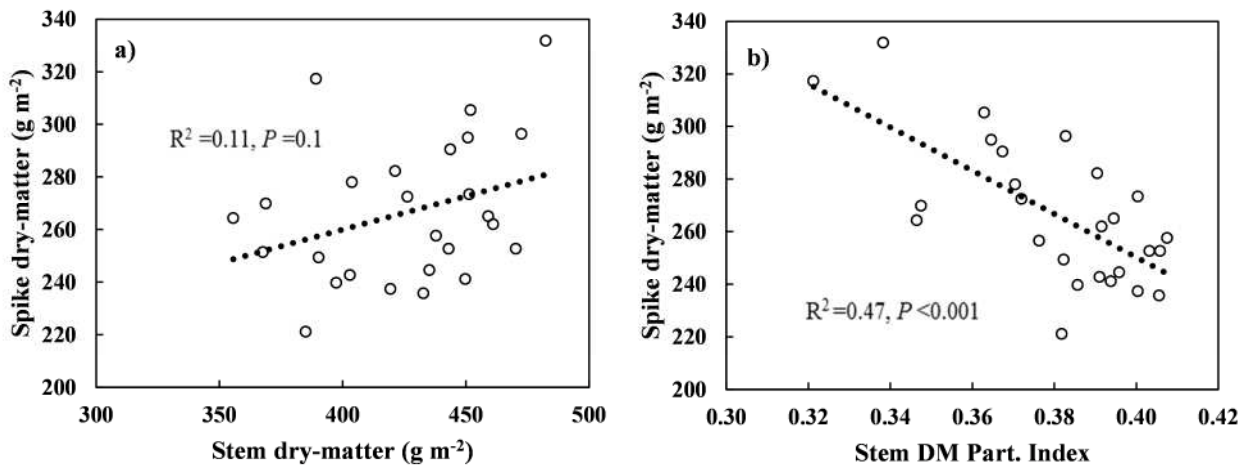
442 DM and length were negatively correlated with SPI for most internodes, with the strongest
 443 associations for Int2 and Int3. IntR DM and length were not associated with SPI (Table 6).
 444 Regarding SW, most stem internodes were not associated with SPI, with the exception of Int3 that
 445 was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

450

451 3.3 DM partitioning traits at anthesis and spike growth and associations with harvest traits

452 Averaging over years, there was no significant association between spike dry-matter (g m^{-2})
453 and stem DM (g m^{-2}) at GS65+7d ($R^2 = 0.11$, $P = 0.1$; Fig. 6a), suggesting a weak allometric
454 relationship between the two organs. On the other hand, SDM was negatively associated with
455 proportion of DM partitioned to the stem ($R^2 = 0.47$, $P < 0.001$; Fig. 6b). With respect to stem-
456 internode DM partitioning, results showed that SDM (g m^{-2}) was negatively associated with the
457 proportion of aboveground DM partitioned to Int2 (Int2 PI; $R^2 = 0.30$, $P < 0.01$) and Int3 (Int3 PI; R^2
458 $= 0.25$, $P < 0.01$) among the 26 cultivars (Fig. 7). No associations were observed between SDM and
459 the Ped PI or IntR PI (Fig. 7).

460



461

462 **Figure 6.** Linear regression of spike dry-matter (g m^{-2}) on a) Stem dry-matter (g m^{-2}) and b) Stem
463 Partitioning indexer GS65+7 days for the 26 CIMCOG cultivars. Values represent means in 2012 and
464 2013.

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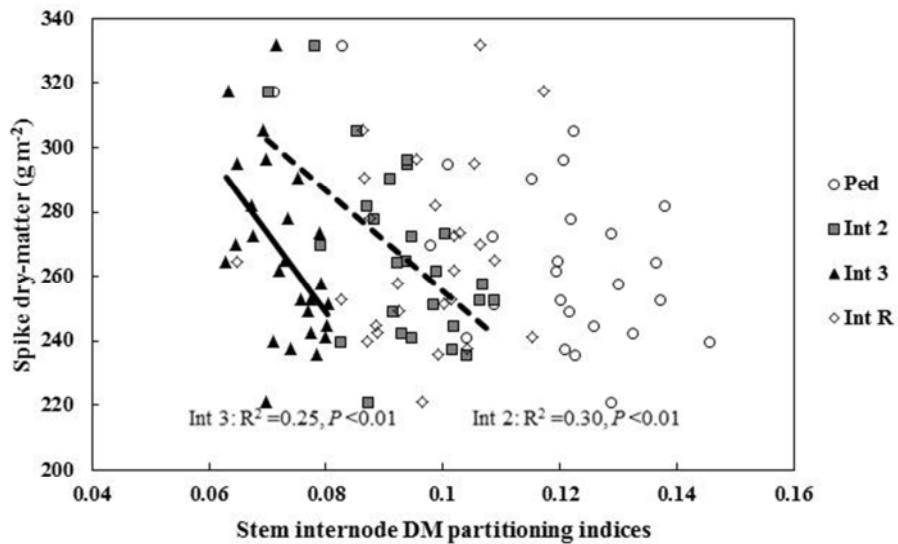


Figure 7. Linear regression of spike DM (g m^{-2}) on stem internode partitioning indices (stem internode DM as a proportion of aboveground DM) for the 26 CIMCOG cultivars.. Values represent means in 2012 and 2013.

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472 Genetic correlations for DM partitioning traits at anthesis and harvest traits are shown in Table 4.
473 Grains m^{-2} and grains per spike were strongly negatively associated with DM partitioning to the stem
474 ($r = -0.55$, $P < 0.001$ and $r = -0.74$, $P < 0.001$; respectively). Dry-matter partitioning to the spike
475 showed a positive association with GPS ($r = 0.52$, $P < 0.01$) but there was association with GN (r
476 $= 0.31$, ns). Thousand grain weight was strongly negatively correlated with SPI ($r = -0.55$, $P < 0.01$)
477 but positively with StPI ($r = 0.72$, $P < 0.01$), similar to the observed relationships between these DM
478 partitioning indices and plant height. Stem internode DM and lengths were negatively and strongly
479 associated with GN for most stem sections, with the exception of IntR ($r = -0.23$, $r = 0.05$, ns,
480 respectively) (Table 6). Thus, stem-internode DM and lengths were positively associated with
481 increasing competition of spike growth and decreasing GN. There was generally a negative
482 association between internode SW and GN, however, this was not significant for Int3 SW (Table 6).
483 From the simple linear regressions, there were no significant correlations between HI and internode
484 characteristics (DM PIs, lengths or SWs).

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 \times 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

518 partitioning and FE. Rachis specific weight (RSW; mg cm⁻¹) was calculated for the subset 17
 519 CIMCOG cultivars in 2013 and there were cultivar differences ($P < 0.001$). Rachis SW showed a
 520 strong negative correlation with FE_H ($r = -0.79$ $P < 0.001$) and a strong positive correlation with GPS
 521 ($r = 0.71$ $P < 0.01$) (Table 6). The genetic correlation coefficient between FE_A and RWS was close to
 522 one (Table 7), due to a high phenotypic correlation coefficient between these traits ($r_p = -0.61$, P
 523 < 0.01 ; not shown) and a low heritability value for FE_A in 2013 ($h^2 = 0.21$; not shown).

524

525 **Table 7.** Non-grain spike DM partitioning at harvest and rachis specific weight (RSW) and genetic
 526 correlations with fruiting efficiency calculated with chaff DM at harvest (FE_H), fruiting efficiency
 527 calculated with spike DM at GS65+7 days (FE_A) and grains per spike (GPS) for a subset of 17
 528 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-SERIM 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

529

^a broad sense heritability.

530

^b CV .: coefficient of variation.

531

^c LSD Gen.: Least significance difference (5%).

532

^dData from 2012 and 2013.

533

^eData 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

538 **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 be linked to greater RUE associated with increased photosynthesis

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 CIMCOG 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

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

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

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

659 Since stem Int2 PI and Int3 PI are difficult to measure in breeders' plots, it is important to
660 identify other morphological attributes indicative of stem DM partitioning in these internodes that
661 breeders could select for to enhance SPI, SDM and HI. In this respect, present results showed that
662 stem internode length is highly associated with internode DM shoot⁻¹. Reducing DM to internode 2
663 and 3 to increase SDM could be aligned with changes in basal internode morphology to maintain
664 minimum requirements for a lodging-proof plant (Piñera-Chavez et al. 2016). In our results, as a
665 single trait stem-internode traits did not correlate significantly with HI. However, a forward stepwise
666 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

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

711

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- 938

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.

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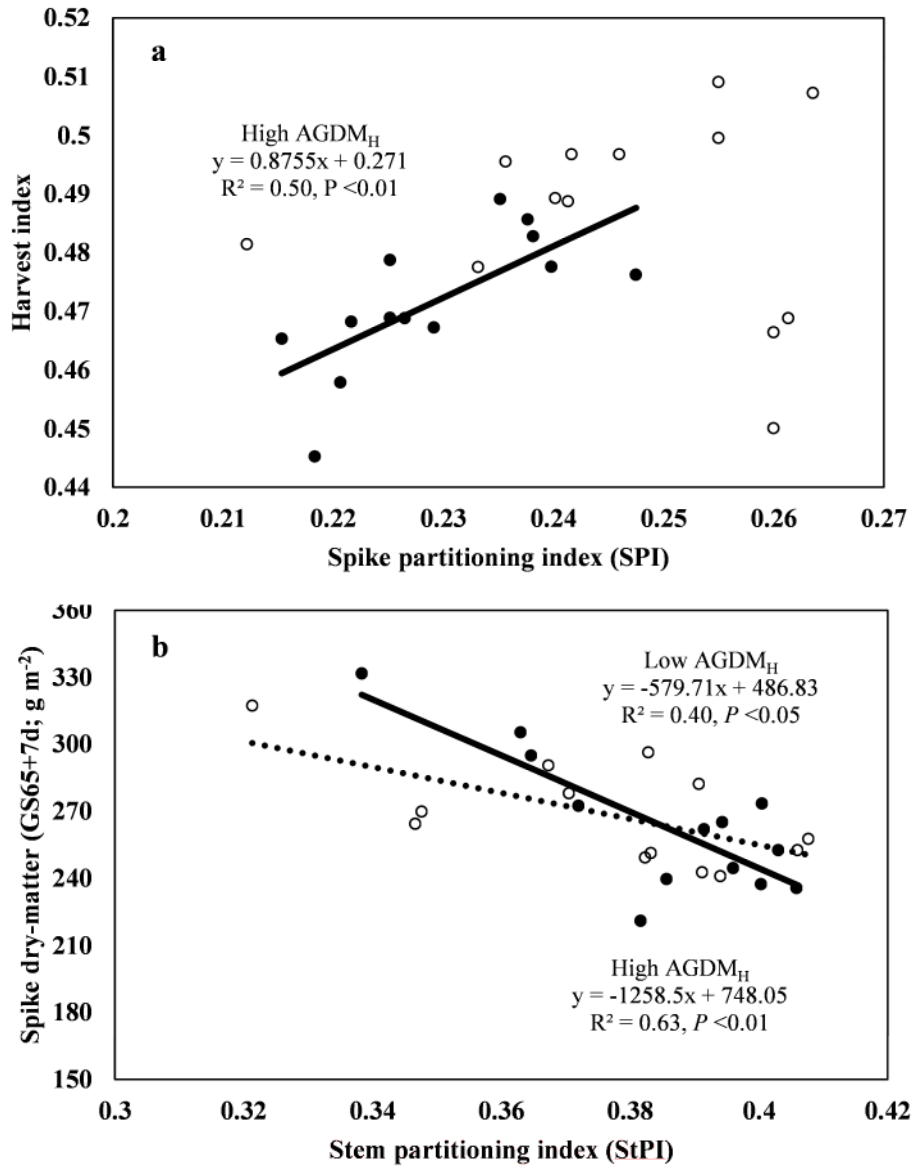
Traits	Variable selected	R ²	Sig.	Variables tested in model
HI	Plant height	7.8	0.049	Plant height, Ped length, Int2 length, Int3
	Int3 PI	21.7	0.021	length, Ped PI, Int2 PI, Int3 PI, Ped SW, Int2 SW, Int 3 SW, AGDM _{A7} .
SPI	Int 3 length	23.06	0.007	Plant height, Ped length, Int2 length, Int3 length,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