

1 **Avoiding lodging in irrigated spring wheat. I. Stem and root structural requirements**

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25 **Abstract**

26 A model of the lodging process has been successfully adapted for use on spring wheat grown in North-West
27 Mexico (NWM). The lodging model was used to estimate the lodging-associated traits required to enable
28 spring wheat grown in NWM with a typical yield of 6 t ha⁻¹ and plant height of 0.7 m to achieve a lodging
29 return period of 25 years. Target traits included a root plate spread of 51 mm and stem strength of the
30 bottom internode of 268 N mm. These target traits increased to 54.5 mm and 325 N mm, respectively, for a
31 crop yielding 10 t ha⁻¹. Analysis of multiple genotypes across three growing seasons enabled relationships
32 between both stem strength and root plate spread with structural dry matter to be quantified. A NWM
33 lodging resistant ideotype yielding 6 t ha⁻¹ would require 3.93 t ha⁻¹ of structural stem biomass and 1.10 t
34 ha⁻¹ of root biomass in the top 10 cm of soil, which would result in a harvest index (HI) of 0.46 after
35 accounting for chaff and leaf biomass. A crop yielding 10 t ha⁻¹ would achieve a HI of 0.54 for 0.7 m tall
36 plants or 0.41 for more typical 1.0 m tall plants. This study indicates that for plant breeders to achieve both
37 high yields and lodging-proofness they must either breed for greater total biomass or develop high yielding
38 germplasm from shorter crops.

39 **Keywords** spring wheat, lodging-proof ideotype, stem strength, anchorage strength, root plate spread, grain
40 yield, stem biomass

41 **Introduction**

42 Lodging is defined as the permanent displacement of plant stems from their vertical position as a result of
43 wind acting on the shoot and rain or irrigation weakening the soil and reducing anchorage strength (Berry et
44 al. 2004). Lodging grain yield reductions of wheat can be in the range of 7 to 80% (Acreche and Slafer,
45 2011; Berry and Spink, 2012; Easson et al., 1993; Fischer and Stapper, 1987; Tripathi et al., 2005; Weibel
46 and Pendleton, 1964) and commonly are accompanied by reductions of bread making quality (Berry et al.
47 2004). In fact, as Pinthus, (1974) indicated, these reductions can be at least as great as that resulting from
48 cryptogamic diseases and insect pests in high yielding environments. Lodging affects all cereal species
49 and many other crops, such as oilseed rape and sunflowers, throughout the world. In wheat, lodging can
50 increase susceptibility to pests and diseases (Berry et al., 2004; Pinthus, 1974), induce negative effects on
51 crop development (decreasing grain per m² and average grain weight) (Acreche and Slafer, 2011; Fischer
52 and Stapper, 1987) and complicate harvest (Berry et al., 2004; Fischer and Stapper, 1987; Pinthus, 1974).
53 Widespread lodging affects from 15 to 20% of the UK wheat growing area once every three or four years

54 (Berry, 1998), although, Griffin, (1998) indicated a lodging incidence of 10% every year. For the Yaqui
55 Valley, a survey conducted during 1981 to 1991 (80 farmers' fields each year) indicated occurrence of
56 lodging from 18 to 40% of the growing area in several years (Tripathi et al., 2004). Yield potential of the
57 Yaqui Valley (NW Mexico) (irrigated environment) has been estimated at 9 t ha⁻¹ and 10.4 t ha⁻¹ for the UK
58 (rainfed environment) (Fischer and Edmeades, 2010). Yield potential losses due to lodging can be
59 estimated from 0.63 to 7.2 t ha⁻¹ for the Yaqui Valley and 0.73 to 8.3 t ha⁻¹ in the UK in the affected area.
60 Peake et al., (2014) estimated a lodging yield potential loss of 1.7 t ha⁻¹ of irrigated spring wheat in sub-
61 tropical Australia (yield potential of 9 t ha⁻¹). In economic terms it has been reported that in a severe
62 lodging year the cost for the farming industry would be around US\$188 million in the UK alone (Berry,
63 1998). For the Yaqui Valley this cost would be US\$29 million (assuming 40% of area affected from 76 000
64 ha (SIAP, 2016), 50% yield loss and US\$215 wheat price per tonne (Lantican et al., 2016)). If we assumed
65 1.0 t ha⁻¹ of yield loss due to lodging in 10% of the world wheat growing area, which was 222 million ha in
66 2014 (Lantican et al., 2016), then there will be a grain yield loss of around 22 million tonnes every year
67 (equivalent to US\$4.7 billion assuming a global wheat price of US\$215). This would add an extra 3% to the
68 700 million tonnes produced in average worldwide every year (FAO, 2014). A wheat crop that would lodge
69 once in 25 years would add an extra 72% to the total worldwide wheat production across those 25 years. In
70 a scenario where the primary objective is to increase grain yield to fulfil global food demands (Reynolds et
71 al., 2012, 2011) and research initiatives such as International Wheat Yield Partnership are investing in this,
72 maintaining lodging resistance will be of paramount importance to protect the increased productivity.

73 Plant breeders have historically reduced lodging risk by introducing dwarfing genes to produce shorter
74 varieties. Additional plant height reduction has been possible through the use of plant growth regulators or
75 PGRs that helped to reduce further lodging risk (Berry et al., 2004; Crook and Ennos, 1995; Pinthus, 1974;
76 Tripathi et al., 2004; Webster and Jackson, 1993). Optimizing crop management also helped farmers to
77 reduce lodging risk and examples are reduced seed rate, delayed sowing, reduced and delayed
78 nitrogen (Berry et al., 2004; Webster and Jackson, 1993) and rolling the soil (Berry et al., 2004). Lodging
79 resistance must be continually improved to counter the escalating lodging risk arising from continued yield
80 increases. However, there may now be limited potential to continue improving lodging resistance through
81 further decreasing plant height because the minimum height that is compatible with high yield (0.7 to 1.0 m
82 (Allan 1986; Kertesz et al. 1991; Richards 1992; Balyan and Singh 1994; Miralles and Slafer 1995a;
83 Flintham et al. 1997; Berry et al. 2014)) has now been reached in many environments. Miralles and Slafer

84 (1995b) suggested that dwarfing genes may have a direct effect to reduce the final grain weight. Dwarfing
85 genes have also been associated with a reduction of water soluble reserves storage capacity (Cossani and
86 Reynolds, 2012) and leaf extension rate (Keyes et al. 1989) that might reduce grain weight. Thus, a
87 reduction of the soluble reserves in the stem (particularly in dry environments) (Borrell et al. 1993) or
88 reduction of final leaf area (McCaig and Morgan, 1993; Daniel J Miralles and Slafer, 1995) and radiation
89 use efficiency at pre-anthesis (Miralles and Slafer, 1997) are possible reasons why extreme dwarfism could
90 significantly reduce grain yield.

91 It therefore seems that reducing height to below 0.7 m might not be the best mechanism to improve
92 lodging resistance in modern high yielding wheat. If we consider that the two types of lodging are due to
93 the bending/buckling of the stem base (stem lodging) or the over-turning of the anchorage system (root
94 lodging), then greater lodging resistance in wheat can be achieved by strengthening these structures (Berry
95 et al. 2003b). In the past, stem strength and anchorage strength have been proposed as key properties of
96 cereal crops for lodging resistance (Crook and Ennos, 1994, 1993; Easson et al., 1995, 1992; Ennos, 1991a,
97 1991b; Graham, 1983; Pinthus, 1974). Large genetic variation has been identified for the anchorage and
98 stem strength of winter wheat in the UK (Berry et al. 2003a; Berry et al. 2007). However, breeding to
99 improve these traits in high yielding wheat requires more understanding about how they develop and
100 possible trade-offs with yield-forming processes in different environments.

101 Baker et al. (1998) developed a model of lodging that has been validated by Berry et al. (2003b) for
102 winter wheat in the UK. The model was based on the interaction of plant, soil and wind characteristics and
103 calculates the stem and root lodging risk according to the wind speed required to over-turn the root
104 anchorage system or to buckle the stem base of a plant. A preliminary attempt to quantify the stem strength
105 and anchorage strength required by winter wheat to withstand 1 in 25 year wind gusts in the UK has been
106 made by Berry et al. (2007) using this lodging model. This indicated that substantial amounts of dry matter
107 may need to be invested in the stem and anchorage system to make plants lodging-proof for a period of 25
108 years, which were estimated at 7.9 t ha^{-1} of stem biomass and 1.0 t ha^{-1} surface root biomass (roots in the
109 first top 10 cm of soil) (Foulkes et al. 2011). This would mean that the maximum harvest index (ratio of
110 grain dry matter to total above-ground dry matter) for a 0.7 m tall crop yielding 8 t ha^{-1} would only be 0.42,
111 rising to 0.50 for a crop yielding 16 t ha^{-1} , which is significantly less than the theoretical maximum harvest
112 index 0.62 estimated by Austin, (1980). Additionally it is possible that the investment in dry matter for the
113 stem and anchorage system during stem elongation which is the critical phase for determination of grain

114 number (Fischer, 1985) may compete for resources with grain yield determination. The implications of
115 Berry et al. (2007) are that the dual requirements of breeding for greater yield and greater lodging resistance
116 will be challenging. However, parts of the analysis were based on limited datasets for winter wheat and it
117 was not possible to distinguish between the structural dry matter and water soluble carbohydrate in the
118 stem, which may mean that the estimate of stem structural dry matter to avoid lodging was over-estimated.

119 The aims of this paper were to 1) investigate the relationship between stem strength and anchorage
120 strength and the dry matter requirements of these structures for spring wheat in North-West Mexico
121 (NWM), 2) adapt an existing model of lodging for winter wheat for spring wheat and calculated lodging
122 risk, 3) estimate the structural dry matter requirements to enable spring wheat to avoid lodging in this
123 particular environment, and 4) consider to what extent the development of structural characteristics may
124 compete with yield-forming processes and grain yield.

125 **Experimental methods**

126 *Experiments*

127 Four field experiments were established during the field seasons 2010-2011, 2011-2012, 2012-2013 and
128 2013-2014 (referred to hereafter as 2011, 2012, 2013 and 2014, respectively) in the experimental station of
129 CENEB (Campo Experimental Norman E. Borlaug) located in the Valle del Yaqui, Sonora, Mexico
130 (27.9°N and longitude 109.9°W). The soil type at the experimental station is a coarse, sandy clay, mixed
131 montmorillonitic typic calciorthid, slightly alkaline (pH 7.7) in nature (Sayre et al. 1997), bulk density of
132 1.32 g cm⁻³ and organic matter of 0.7 % approximately (CIMMYT internal records). Detailed information
133 about experiments and cultivars (CIMMYT Mexico Core Germplasm Panel or CIMCOG consisting of 58
134 *T. aestivum* and two *T. durum* and described in Table S1) is given in a companion paper by (Piñera-Chavez
135 et al., (2016). The whole CIMCOG panel was established during 2011 and a subset of 30 cultivars were
136 used for 2012 and 2013 (as indicated in Table S1). Experiments were managed under a conventional
137 agricultural management but maintaining yield potential conditions. The average seed rate for all plots in
138 experiments 2011, 2012 and 2013 was 10.6 g m⁻² which gave a range 213-292 seeds m⁻². For the
139 experiment in 2014 a subset of five cultivars with contrasting values for stem strength, anchorage strength
140 and stem wall material strength (cultivars 7, 19, 24, 57 and 60, see Table S1) was established using seed
141 rates of 75, 125 and 175 seeds m⁻² to evaluate the effect of low plant populations on lodging traits. The
142 irrigation schedule included five to six flood irrigation events (including one at sowing) during the cycle

143 and the fertilization was 200 kg ha⁻¹ of N (25 % before sowing and 75 % before first irrigation event) and 50
 144 kg ha⁻¹ of P (before sowing). Plant growth regulators were not applied in any of the experiments. Plant
 145 emergence dates (at 50 % of plants emerged) were recorded at 15 of December 2010, 16 of December 2011,
 146 02 of December 2012 and 01 of December 2013 for experiments 2011, 2012, 2013 and 2014, respectively.

147 *Measurements*

148 Plant measurements were done at GS65 + 20 days (Zadoks et al. 1974) during 2011, 2012 and 2013 as was
 149 described in (Piñera-Chavez et al., 2016) (detailed key information of measurements is given in Table S2).
 150 Additionally, during 2013 and 2014 main shoot measurements of the length and breaking strength
 151 following removal of the leaf-sheath of the internodes 1 to 5 were determined for five cultivars with
 152 contrasting performances in stem strength, material strength and anchorage strength (Table 1). Internode 1
 153 in the main shoot was identified, defined as the first internode of more than 10 mm, originating at or just
 154 below the ground surface and without crown roots emerging from its upper node. Subsequent internodes
 155 ascending the stem were numbered two, three, four etc., with the uppermost internode referred to as the
 156 peduncle. Also, dry weight and the following determination of the water soluble carbohydrates content
 157 (WSC) was made on these internodes. WSC content was also determined for the whole main shoot in all
 158 cultivars used for experiments 2011, 2012 and 2013. These analyses were carried out in the Maize Nutrition
 159 Quality and Plant Tissue Analysis Laboratory from CIMMYT (El Batán, Mexico) using the Anthrone
 160 method (Galicía et al. 2008).

161 **Table 1** Cultivars from CIMCOG used for 2014 experiment

Cultivar	Character of interest
BACANORA T 88 ^a	Lowest stem and anchorage strength
CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6/RIALTO ^a	Highest anchorage strength
CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2 ^a	Highest material strength
WBLL1*2/KURUKU*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA(213)//PGO/4/HUITES ^a	Highest stem strength
YAV_3/SCO//JO69/CRA/3/YAV79/4/AE.SQUARROSA(498)/5/LINE1073/6/KAUZ*2/4/CAR//KAL/B B/3/NAC/5/KAUZ/7/KRONSTAD F2004/8/KAUZ/PASTOR//PBW343 ^a	Lowest material strength

162

163 *Calculations*

164 A validated model of lodging for winter wheat (Baker et al. 1998; Berry et al. 2003b) was used to calculate
 165 the stem failure moment (stem strength at the point of failure), anchorage failure moment (anchorage
 166 strength at the point of failure), the wind-induced base bending moment (leverage force) of the shoot and
 167 plant, and overall risk to stem and root lodging on spring wheat (stem and anchorage failure wind speed).
 168 This model included stem base bending model estimation using Baker, (1995) method and a simplified
 169 version of the root strength model of Crook and Ennos, (1993).

170 The stem failure moment (B_s) was calculated from the breaking strength (F_s) and length (h) of the
 171 internode (Eq. 1).

$$172 \quad B_s = \frac{1}{4} F_s h \quad (1)$$

173 Anchorage failure moment (B_R) was calculated from the root plate spread (d), the shear strength of the
 174 surrounding soil (s) and a constant of 0.43 (k_3) taken from Baker et al. (1998) (Eq. 2). The surrounding soil
 175 was assumed to be at field capacity with a shear strength of 6 kPa (Baker et al. 1998).

$$176 \quad B_R = k_3 s d^3 \quad (2)$$

177 The shoot base bending moment (B) was obtained from the density of air ($\rho = 1.2 \text{ kg m}^{-3}$), the projected
 178 ear area (A), the shoot's height at centre of gravity (X), the wind gust speed (V_g), the shoot's natural
 179 frequency (n), the acceleration due to gravity ($g = 9.81 \text{ m s}^{-2}$), the shoot's damping ratio ($\xi = 0.08$) and the
 180 drag coefficient of the ear ($C_d = 1.0$). The base bending moment of the whole plant was calculated by
 181 multiplying B by the number of shoots per plant (Baker et al. 1998):

$$182 \quad B = \frac{1}{2} \rho A C_d X V_g^2 \left(1 + \frac{g}{(2\pi n)^2 X} \right) \left(1 + e^{-\pi \xi} \frac{\sin(\pi/4)}{\pi/4} \right) \quad (3)$$

183 Natural frequency is considered a parameter of major importance of the wind-induced leverage (base
 184 bending moment) (Baker et al., 1998), although, height at centre of gravity and ear projected area have also
 185 a great influence (Berry et al., 2003b). Assuming the wind-induced leverage decreases linearly for
 186 progressively higher positions up the stem (Berry et al. 2006), bending moment at the base of subsequent
 187 internodes 2 to 5 was calculated by multiplying the leverage exerted at the base of internode 1 with the ratio
 188 of the distance between the base of internodes 2, 3, 4 or 5 and the mid-point of the ear with the total stem
 189 height at the mid-point of the ear (Berry et al. 2007). These ratios were measured in spring wheat at 0.84 for
 190 the base of internode 2, 0.70 for internode 3, 0.50 for internode 4 and 0.19 for internode 5. Ratio at the mid-
 191 point of the length internode 5 or peduncle was used to calculate the bending moment (19%) due to non-

192 uniform geometric properties (Berry et al. 2007). This means that the leverage exerted at the base of
 193 internodes 2, 3, 4 and the peduncle should be 84, 70, 50 and 19 %, respectively, of the leverage exerted at
 194 the base of internode 1.

195 The stem failure wind speed (V_{gS}) and the anchorage failure wind speed (V_{gR}) were calculated by
 196 combining and re-arranging equations (1) and (2), with equation (3) (Berry et al., 2003b). Letter N in
 197 equation (5) indicates the number of shoots per plant.

$$198 \quad V_{gS} = (2B_s)^{0.5} \times \left(\rho A C_d X \left(1 + \frac{g}{(2\pi n)^2 X} \right) (1 + K_\xi) \right)^{-0.5} \quad (4)$$

$$199 \quad V_{gR} = (2NB_R)^{0.5} \times \left(\rho A C_d X \left(1 + \frac{g}{(2\pi n)^2 X} \right) (1 + K_\xi) \right)^{-0.5} \quad (5)$$

200 *Statistical analysis*

201 Simple linear and non-linear regression analysis and simple linear regression analysis with groups were
 202 used to investigate relationships between traits. Analysis of variance using a general linear model was used
 203 to test for differences between years, cultivars and leaf sheath removal treatments together with treatment
 204 interactions. All the analyses were carried out by GENSTAT 15th Edition (VSN International, 2012).

205 *Wind speed characterisation*

206 Daily wind run data was sourced from a local meteorological station within the wheat growing area of the
 207 Valle del Yaqui, Sonora, Mexico (grid reference 27.3°N and 109.1°W, 38 m asl) spanning a 40-year period
 208 from 1973 to 2013. The weather station was located within 10 km from the experiments. The daily wind run
 209 data were converted to the maximum hourly mean wind speed for each day by multiplying by a factor of
 210 1.606 (Berry et al. 2003b). The hourly mean values were each converted to hourly gust values, for gusts of
 211 duration $\tau = 0.3$ s, using the empirical equation described by Berry et al. (2003b):

$$212 \quad U_{gust} = U_m \left(1 + 0.42 \left(\frac{\sigma}{U_m} \right) \sin \left(\frac{3600}{\tau} \right) \right) \quad (6)$$

213 where σ/U_m is the turbulence intensity (TI). A value of $\sigma/U_m = 0.5$ was used, again following the work of
 214 Berry et al. (2003b) who used the value determined by Finnigan (1979) for wind over a wheat crop. These
 215 values were then corrected for differences in the roughness, z_0 , at the airport weather stations and the crop
 216 locations, and also for the difference in height above ground, z , of the airport anemometers (10 m), the met

217 station anemometer (1.5 m) and the pertinent wind speed height for crop lodging of 2 m (Baker et al. 1998;
218 Berry et al. 2003b). This correction takes the form:

$$219 \quad U_c = U_w \frac{\ln\left(\frac{z-d}{z_0}\right)_c}{\ln\left(\frac{z-d}{z_0}\right)_w} \quad (7)$$

220 where subscripts c and w refer to the crop and weather station locations, respectively. z_0 over the crops has
221 been estimated as $z_0 = \lambda(h - d)$, where $\lambda = 1/3$, $h = 1$ m and $d = 0.75h$, giving a value of $z_0 = 1/12$ m, with z_0
222 = 0.01 m at the weather station (Berry et al. 2003b). Finally, an altitude correction has been applied to the
223 gust wind speed using the V_{99} correction factor of $(1 + 0.009h)$ specified in Baker et al. (1998). The
224 correction is taken as the ratio $(1 + 0.009h_c)/(1 + 0.009h_w)$ where h_c and h_w are the crop and weather station
225 altitudes respectively. As stated in Berry et al. (2003b), these methods were developed based on UK
226 Meteorological Office data and should therefore be applied with care in other locations. In particular, these
227 methods are only applicable where synoptic (non-convective) winds are expected.

228 In order to allow the analysis to concentrate on the period when lodging risk is possible, the hourly gust
229 values were split by month (i.e. 12 groups of data were formed from the 40 years of data, each
230 corresponding to a particular month). The probability of the gust speed exceeding a certain value was
231 calculated for each month on a per day basis. At each scale, probabilities of the gust speed being within a
232 certain range were calculated by sorting the values into 0.5 m s^{-1} wide “bins”, with the probability of gusts
233 within the range covered by each bin calculated simply from the number of values in that bin divided by the
234 total number of values. Probabilities of exceeding a certain value were calculated as the sum of the
235 probabilities for the bins whose ranges exceeded the required value. The probability of experiencing any
236 particular wind gust during the lodging risk period was then calculated using daily gust speed probabilities
237 for the months during which lodging is possible and assuming a stem lodging risk period of 50 days in
238 March and April (assuming one wheat cycle per year) (window between cultivars with earliest flowering
239 and the latest maturity was 52 days). Root lodging risk increases when the soil surface is wet (Easson et al.
240 1995; Berry et al. 2003a), typically when the first 50 mm of soil is at field capacity (Baker et al. 1998). This
241 can be attributed to the movement of the plant crown in a saturated soil surface after flood irrigation in
242 irrigated environments (Fischer and Stapper, 1987) or after precipitation in rainfed environments (Crook
243 and Ennos, 1994). Moreover, Sterling et al. (2003), using a portable wind tunnel in the field, found that root
244 lodging occurred only when the soil was saturated. Additionally, it is well known that water supply most
245 spring wheat worldwide is given by flood irrigation in flat beds. It therefore seems sensible to consider the

246 root lodging risk when the soil surface is moist. For our purposes, we estimated the root lodging risk period
247 for the NWM environment to be 10 days, based on the number of days when the first 60 mm of soil depth
248 (maximum root plate depth exceeded 50 mm in CIMCOG panel) was at 50% of plant available water
249 during the 50 day lodging risk period. At lower soil moisture content, the soil is usually too strong to permit
250 root lodging. Spring wheat in this region typically receives three flood irrigation events during the 50 day
251 lodging risk period, each delivering approximately 73 mm water (0 – 120 cm soil core depth). Windy
252 conditions often occur post-anthesis which may coincide with irrigations indeed in that period in 2014 and
253 2016 windstorms affected the area. Farmers pay special attention whether to apply the last irrigation or not
254 (normally at mid grain filling) because of the intensity of the windy season. This is a difficult decision to
255 make because avoiding the last irrigation sometimes ends in grain yield losses. Using internal records of
256 field capacity and permanent wilting point from CENEB and evapotranspiration data from nearest weather
257 station it has been estimated that the top 150 mm of soil dries to 50 % of plant available water after 8 days
258 of irrigation. The soil tends to dry from the top downwards which indicates that the top 60 mm of soil will
259 be dried to 50% plant available water within about 3.2 days, giving about 10 days when the top 60 mm of
260 soil may be moist and weak enough to permit root lodging. A review of rainfall data over the past 40 years
261 showed that the chance of more than 10 mm of rain (enough to bring the top 60 mm of soil to field
262 capacity) falling in one day during March or April was very small.

263 *Lodging model development*

264 This section describes how for spring wheat the lodging model was further developed to estimate the key
265 plant characteristics that determine base bending moment (shoot height at centre of gravity, shoot natural
266 frequency and ear area) from plant characteristics that are more commonly measured by crop physiologists
267 (grain yield, grain harvest index, plant height and shoots m^{-2}). This process was carried out for winter wheat
268 by Berry et al. (2004), however spring wheat has fundamental differences which may affect how the plant
269 characteristics described above are related. One key difference is the presence of awns on the spring wheat
270 varieties. Theoretically, shoot height at centre of gravity (X) can be calculated from stem length (S_L), stem
271 and leaf fresh weight (S_W), ear fresh weight (E_W) and ear length (E_L) following the Eq. (8) which assumes
272 uniform weight of shoot and ear (Berry et al. 2004).

$$273 \quad X = \frac{(S_L S_W + 2S_L E_W + E_L E_W)}{2(S_W + E_W)} \quad (8)$$

274 The components of Eq. (8) can be calculated from physiological crop traits measured commonly: grain
 275 yield (Y , g m^{-2}), the number of ears per metre square (E_n), the ratio of chaff dry weight to total ear dry
 276 weight (α), the harvest index (HI) and the crop height to the tip of the ear (h , m) (Eqs. 9 – 11).

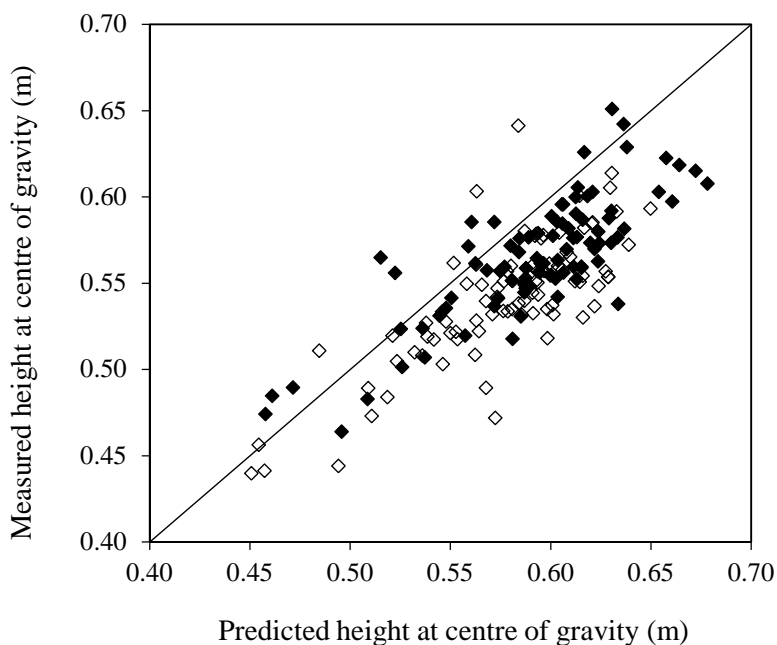
$$277 \quad E_W = \frac{Y/(1-\alpha)}{E_n} \quad (9)$$

$$278 \quad S_W = \frac{E_W(1-\alpha)}{HI} - E_W \quad (10)$$

$$279 \quad S_L = h - E_L$$

$$280 \quad (11)$$

281 Equation 8 was tested using measurements of S_W and E_W at GS65 + 7 d in a random sample of 20 plants
 282 per plot, and X , S_L , E_n and E_L at GS65 + 20 d in 10 plants per plot in all the plots during 2012 and 2013
 283 experiments. Fig. 1 shows that Eq. 8 accounted for a substantial proportion of the differences in height at
 284 centre of gravity, but over-predicted the measurement by about 6% on average. The most likely explanation
 285 for the overestimate is non-uniform distribution of the dry matter along the shoot, with more at the base
 286 than the top (Berry et al. 2004).



287

288 **Fig. 1** Predicted and measured height at centre of gravity at GS65 + 7 days and GS65 + 20, respectively, for
 289 plot means of 2012 (closed squares) and 2013 (open squares). (—) 1:1 line. Best fit line, $y = 0.70x + 0.15$;

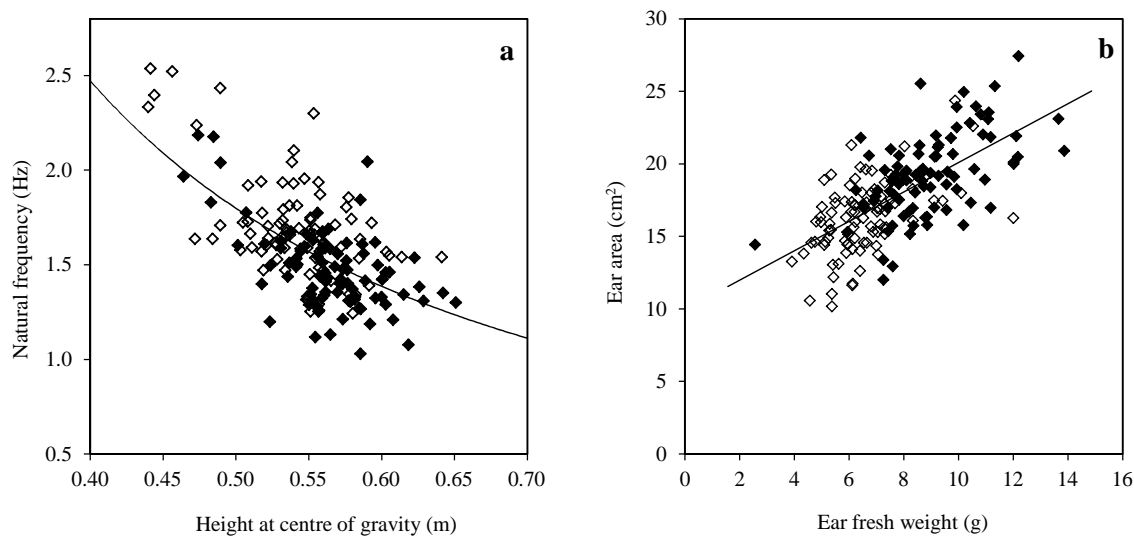
290 $R^2=0.64$ ($P < 0.001$)

291 Regression analysis performed with data from all plots measured in 2012 and 2013 showed an inverse
 292 correlation between the natural frequency (n_n) of the main shoot with the measured height at centre of
 293 gravity (Fig. 2a) resulting in equation 12. The ear area (including awns) was shown to correlate with the
 294 fresh weight of the ear resulting in equation 13 (Fig. 2b).

295 $n_n = 0.7x^{-1.4} + 0.3$

296 (12)

297 $A = 9.95 + 1.02E_w$ (13)



298

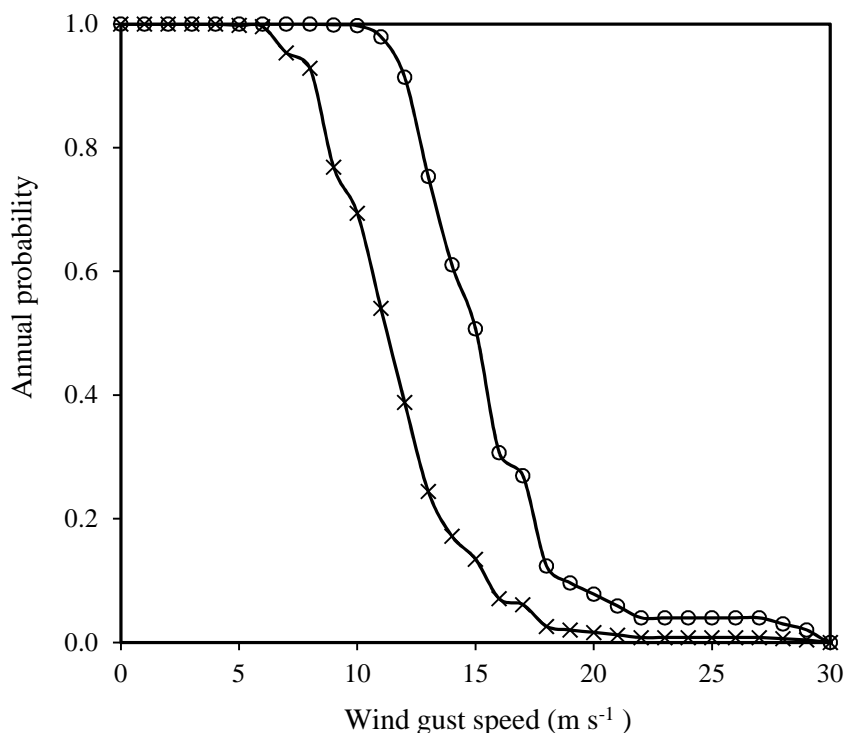
299 **Fig. 2** (a) Height at centre of gravity at GS65 + 20 plotted against natural frequency for plot means of 2012
 300 (closed squares) and 2013 (open squares). Regression line: $y = 0.67x^{-1.4}$ ($R^2=0.38$; $P < 0.001$). (b) Ear fresh
 301 weight plotted against ear area at GS65 + 20, for plot means of 2012 (closed squares) and 2013 (open
 302 squares). Best fit line: $y = 1.02x + 9.95$ ($R^2=0.44$; $P < 0.001$)

303 Hence, the further developed equations 8 to 13 for spring wheat have demonstrated how plant height,
 304 harvest index, shoots per square meter and yield can be used to calculate lodging model inputs; height at
 305 centre of gravity, natural frequency and ear area. Successively, these parameters can be used in equation 3
 306 to estimate the effect of changes to plant height, harvest index and yield on the base bending moment of a
 307 single shoot and the whole plant on spring wheat genotypes.

308 Results

309 *Wind gust speed probabilities*

310 The probabilities for experiencing wind gust speeds at the height of the crop during stem and root lodging
 311 risk periods at NWM are summarised in Fig. 3.



312

313 **Fig. 3** North-West Mexico seasonal maximum wind gust probabilities for 50 days of high stem lodging risk
 314 (○) and for 10 days of high root lodging risk (when surface soil horizon is moist) (×)

315 Annual wind gust speed return periods for the NWM environment (Table 2) show that the plant must
 316 withstand a wind gust of 22 m s⁻¹ to have a stem lodging return period of 25 years, and it must withstand a
 317 wind speed of 18 m s⁻¹ to have a root lodging return period of 25 years. For a return period of 10 years the
 318 critical wind speeds that must be withstood fall to 19 m s⁻¹ and 16 m s⁻¹ for stem and root lodging,
 319 respectively. Considering lodging return period as the period of time between lodging events or the period
 320 of time between two wind gust peaks of 22 m s⁻¹ (stem lodging) and 18 m s⁻¹ (root lodging) if we use a
 321 lodging return period of 25 years (comparable with the UK lodging resistant ideotype). Berry et al., (2004)
 322 defined lodging proofness as: “the structure that can withstand the strongest wind likely to occur over a
 323 cereal crop once every generation”.

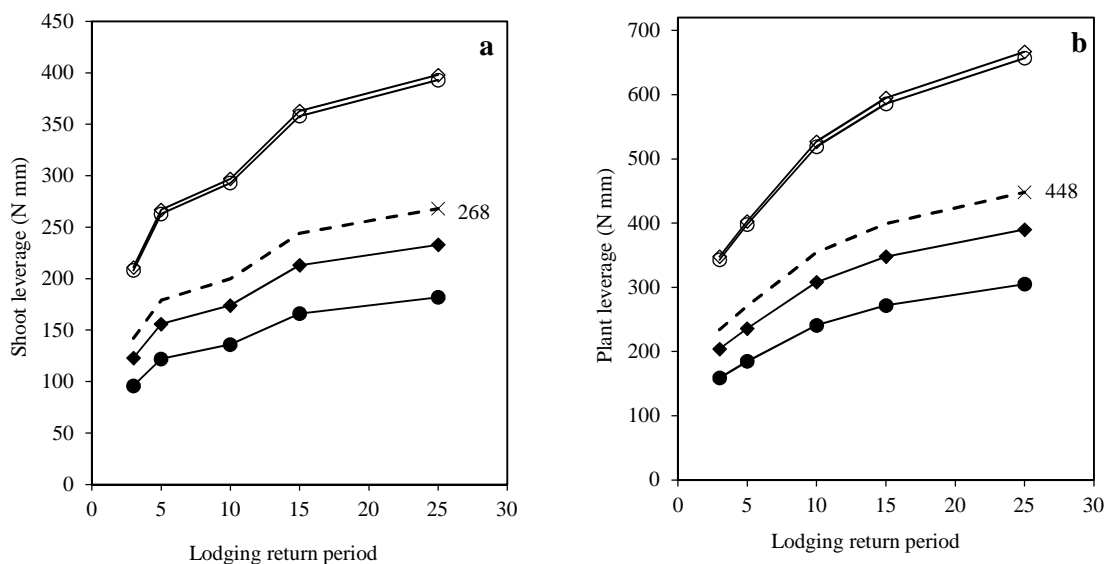
324 **Table 2** Seasonal wind gust speed return period for Obregon

Wind gust return period (years)	Wind gust speed (m s ⁻¹)	
	stem lodging risk	root lodging risk
5	18	14
10	19	16
15	21	17

325

326 *Calculating the lodging-proof ideotype*

327 The maximum wind induced shoot and plant leverages for crops with a range of crop height and yield have
 328 been calculated for lodging return periods of 1 year in 5 to 1 year in 25 (Fig. 4) using equations 3 and 6-11.
 329 The wind-induced shoot base bending moment (leverage) (N mm) calculated for the maximum wind speed
 330 expected during the entire 50 day stem lodging risk period represent the minimum failure moment (stem
 331 strength) of the stem base (N mm) for supporting the shoot. The wind induced plant leverage calculated for
 332 the wind speeds expected during the 10 day root lodging period represent the minimum strength of the
 333 anchorage for supporting all the shoots of a single plant. To carry out these calculations it was assumed that
 334 the crops had 500 shoots per plant and 200 plants m^{-2} which are typical for the Yaqui Valley near Obregon.
 335 The ideotype crop with the current average on farm yield of $6 t ha^{-1}$ (at 12% moisture) for the NWM
 336 environment (Fischer and Edmeades, 2010), and minimum crop height of 0.7 m that has been observed to
 337 be compatible with high yield, must have a stem strength equivalent to the 268 N mm of shoot leverage and
 338 anchorage strength equivalent to 448 N mm of plant leverage. If crop yield and plant height are increased to
 339 $10 t ha^{-1}$ and 1.0 m, respectively, then the stem strength required must be equivalent to 480 N mm of shoot
 340 leverage and anchorage strength equivalent to 803 N mm of plant leverage.



341

342 **Fig. 4** Shoot leverage (a) and plant leverage (b) for a crop yielding $6 t ha^{-1}$ with a crop height of 1.0 m (○)343 and 0.5 m (●), and crop yielding $16 t ha^{-1}$ (◇) and $4 t ha^{-1}$ (◆) with a crop height of 0.7, for different lodging

344 return periods in the NWM environment. Dotted line indicates a NWM wheat crop with current average
 345 yield of 6 t ha⁻¹ and putative minimum crop height compatible with this yield of 0.7 m

346 The size of the root plate required to avoid lodging for a range of crop types and lodging return periods
 347 have been calculated using Eq. (2). Stem material strength (σ) was calculated using Eq. (14) where stem
 348 wall width (t) was constant (0.65 mm) and the stem radius (a) and stem strength (Bs) were defined by the
 349 maximum wind gust of each lodging return period (Table 2). A minimum stem wall width of 0.65 mm was
 350 assumed because it is understood that a thin walled, but wide, cylinder is the best way of achieving strength
 351 for the minimum investment of dry matter (Berry et al., 2007) and 0.65 mm was the thinnest wall width
 352 observed in the spring wheat experiments.

$$353 \quad Bs = \frac{\sigma \pi a^3}{4} \left(1 - \left(\frac{a-t}{a} \right)^4 \right) \quad (14)$$

354 The target root plate spread ranged from 43.2 mm for a 0.7 m tall crop yielding 6 t ha⁻¹ with a lodging
 355 return period of 5 years, to 62.1 mm for a 1.0 m tall crop yielding 10 t ha⁻¹ with a lodging return period of
 356 25 years. These calculations assumed the soil was rolled after sowing to consolidate it. A 0.7 m tall crop
 357 yielding 6 t ha⁻¹ with a lodging return period of 5 years would require a stem diameter of 4.04 mm with a
 358 material strength of 35 MPa or alternatively the required strength could be achieved with a stem diameter of
 359 3.51 mm with a material strength of 50 MPa. A 1.0 m tall crop yielding 10 t ha⁻¹ with a lodging return
 360 period of 25 years would require a stem diameter of 6.09 mm with a material strength of 35 MPa or 5.24
 361 mm with a material strength of 50 MPa (Table 3).

362 **Table 3** NWM ideotype trait targets for different lodging return periods

Character	Lodging return period (years)			
	5	10	15	25
	0.7 m tall and 6 t ha ⁻¹			
Root plate spread (mm)	43.2	47.3	49.2	51.1
^a Internode diameter (mm)	4.04	4.23	4.58	4.76
^b Internode diameter (mm)	3.51	3.67	3.97	4.12
	0.7 m tall and 10 t ha ⁻¹			
Root plate spread (mm)	46.1	50.4	52.5	54.5
^a Internode diameter (mm)	4.38	4.58	4.97	5.16
^b Internode diameter (mm)	3.79	3.96	4.29	4.45
	1.0 m tall and 6 t ha ⁻¹			
Root plate spread (mm)	49.1	53.7	55.9	58.1
^a Internode diameter (mm)	4.73	4.94	5.38	5.59
^b Internode diameter (mm)	4.09	4.27	4.63	4.82
	1.0 m tall and 10 t ha ⁻¹			

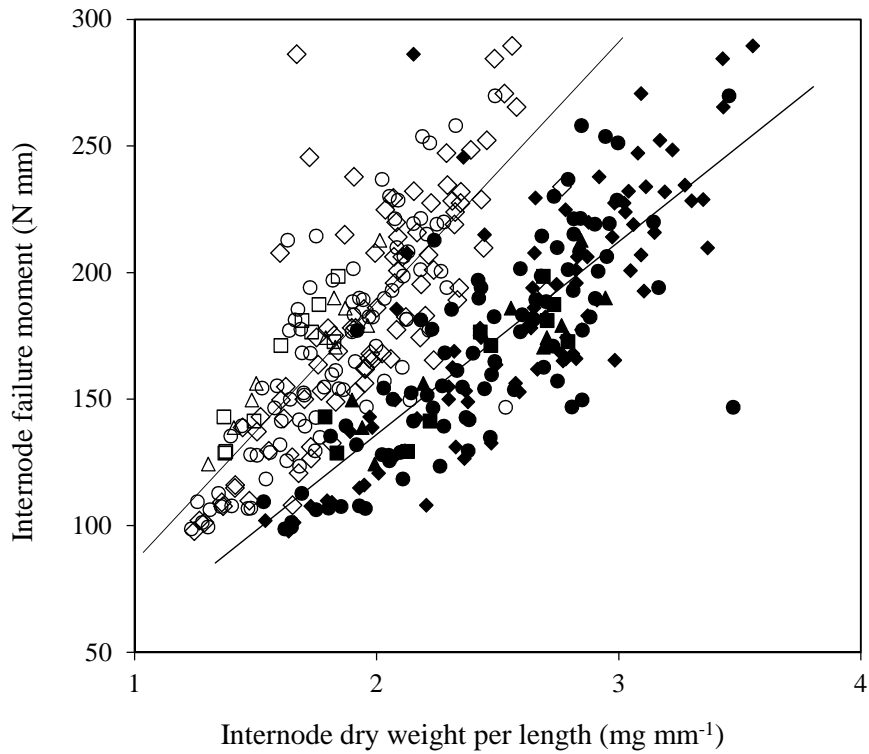
Root plate spread (mm)	52.5	57.4	59.8	62.1
^a Internode diameter (mm)	5.14	5.38	5.85	6.09
^b Internode diameter (mm)	4.43	4.63	5.03	5.24

363 ^a Material strength of 35 Mpa; ^b material strength of 50 Mpa; * all crops assumed to have a stem wall width of 0.65 mm

364 *Biomass and failure moment of stem and anchorage system*

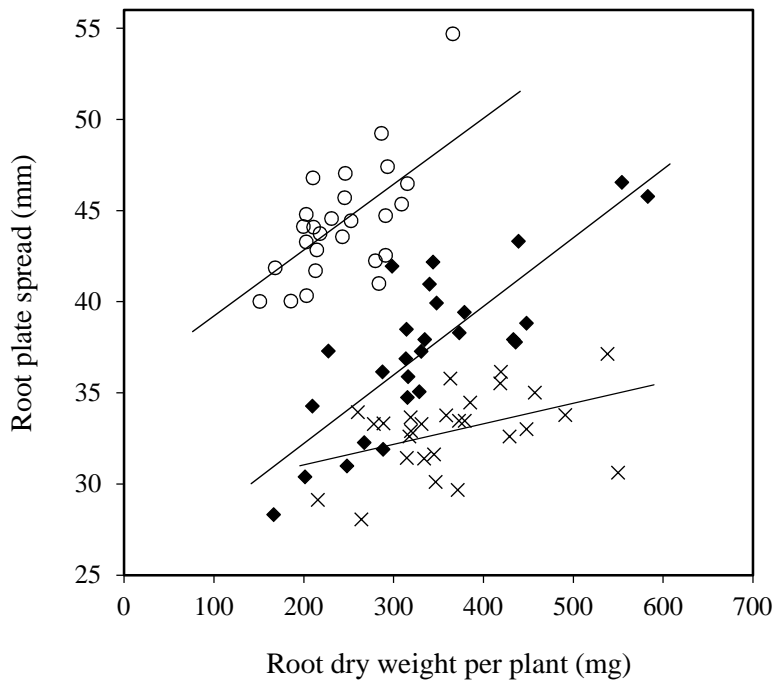
365 A positive regression ($R^2 = 0.63$; $P < 0.001$) was found between the structural stem dry matter per unit
366 length and internode failure moment for internodes 1 to 2 (27 cultivars, 2011, 2012, 2013 and 5 cultivars,
367 2014) and internodes 3 to 4 (5 cultivars, 2013 and 2014). According to this regression model where the
368 response variable was the internode failure moment (stem strength), a fitted value of 100 N mm in this
369 parameter could be achieved with a structural stem dry weight per unit length of 1.13 mg mm^{-1} or with 1.53
370 mg mm^{-1} of structural plus WSC stem dry weight (Fig. 5). There was no association between WSC content
371 and internode failure moment for internodes 1 to 2 (2011, 2012, 2013 and 2014) and internodes 3 to 4 (2013
372 and 2014) ($R^2 = 0.009$).

373 Regarding the anchorage system there was a positive relationship between root dry weight per plant and
374 root plate spread among 27 genotypes which had a consistent slope across years 2012 and 2013 of 0.038
375 mm mg^{-1} , but different y axis intercepts of 24.7 and 35.6 mm, respectively, and an R^2 of 0.74 ($P < 0.001$)
376 for the regression model (Fig. 6). Regression analysis on this association for 2011 showed a fitted line with
377 a slope of 0.011 mm mg^{-1} and y-axis intercept of 28.8 mm and an R^2 of 0.18 ($P < 0.05$).



378

379 **Fig. 5** Dry weight per unit length plotted against internode failure moment of internode 1 (diamonds),
 380 internode 2 (circles) for 27 genotypes (2011, 2012 and 2013 experiments) and of internodes 1, internode 2,
 381 internode 3 (triangles) and internode 4 (squares) for five genotypes (2013 and 2014 experiments). Open
 382 figures indicate structural dry weight ($y = 103x - 16.8$; $R^2 = 0.63$; $P < 0.001$) and closed figures indicate
 383 overall dry weight ($y = 76.2x - 16.3$; $R^2 = 0.64$; $P < 0.001$)



384

385 **Fig. 6** Surface root dry weight per plant plotted against root plate spread of 27 spring wheat genotypes.

386 Parallel model for (♦) 2012 experiment ($y = 0.038x + 24.7$) and (○) 2013 experiment ($y = 0.038x + 35.6$);

387 $R^2 = 0.74$; $P < 0.001$). Experiment (×) 2011 showed a regression line of $y = 0.011x + 28.8$ with an R^2 of

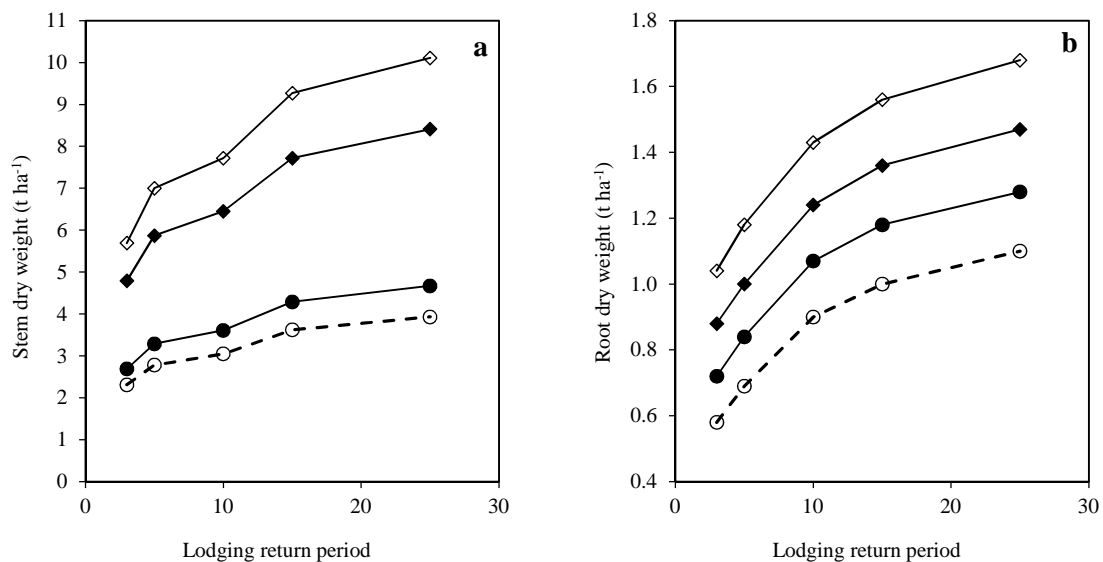
388 0.18 ($P < 0.05$)

389 Experiments in 2013 and 2014 included a screening of five genotypes which were evaluated for
 390 internode failure moment with and without the leaf sheath. Analysis of variance showed that removing the
 391 leaf sheath significantly reduced the internode failure moment by 8 N mm, 23 N mm, 32 N mm, 31 N mm
 392 and 47 N mm for internodes 1, 2, 3, 4 and 5, respectively (4, 12, 19, 19 and 34%, respectively). This
 393 variation was statistically significant ($P < 0.05$) for internodes 2 (SED = 5.55), 3 (SED = 4.97), 4 (SED =
 394 4.81) and 5 (SED = 4.38). Differences between cultivars were found for all internodes (SED 7.94, $P <$
 395 0.001) and there were no significant interactions between cultivar and leaf sheath treatments.

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

397 The amount of structural stem and surface root dry matter required to resist lodging for a range of crop
 398 types and lodging return periods are described in Fig. 7. The structural stem biomass required to achieve
 399 specified lodging return periods was first estimated for each individual internode using the empirical
 400 equation $y = 103x - 16.8$ from Fig. 6 for 2011-14 data, where the “y” value was the leverage exerted at the

401 base of each internode and the “x” value was the structural dry weight per unit length. The structural dry
 402 weight of each internode was calculated by multiplying the dry weight per unit length by the internode
 403 length. The structural dry weight of the whole stem was calculated by summing the dry weights of all five
 404 individual internodes. The target structural stem biomass ranged from 2.78 t ha⁻¹ for a 0.7 m tall crop
 405 yielding 6 t ha⁻¹ with a lodging return period of 5 years to 10.1 t ha⁻¹ for a 1.0 m tall crop yielding 10 t ha⁻¹
 406 with a lodging return period of 25 years. Root biomass was estimated by first calculating the root plate
 407 spread required to withstand the wind induced plant leverage, then using empirical equation $y = 0.038x +$
 408 30.2 from Fig. 6 for 2012-13 data, where the “y” value is the root plate spread and the “x” value is the
 409 surface root biomass per plant. The target root biomass ranged from 0.69 t ha⁻¹ for a 0.7 m tall crop yielding
 410 6 t ha⁻¹ with a lodging return period of 5 years to 1.68 t ha⁻¹ for a 1.0 m tall crop yielding 10 t ha⁻¹ with a
 411 lodging return period of 25 years.

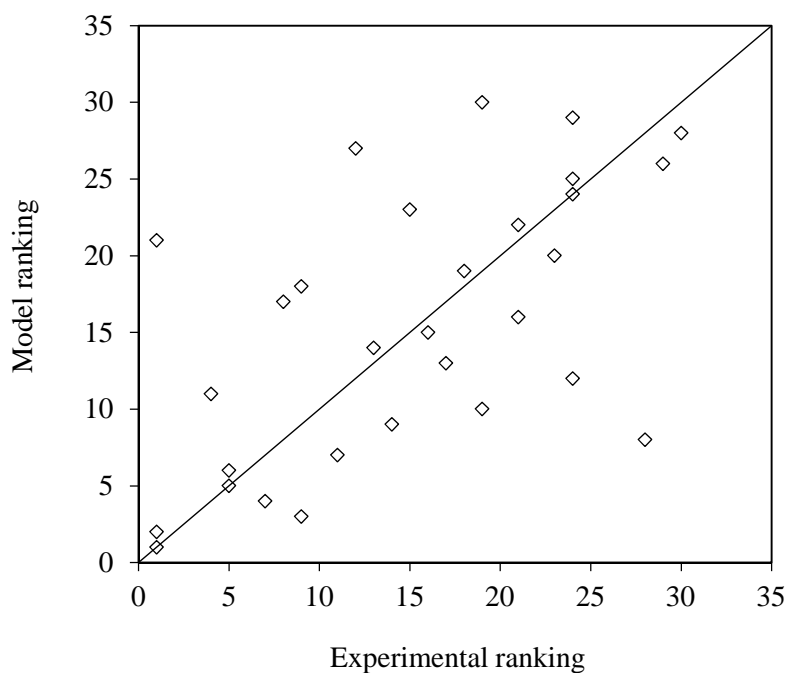


412
 413 **Fig. 7** Stem (a) and root dry weight (b) for a crop yielding 6 t ha⁻¹ with a crop height of 1.0 m (◆) and 0.7 m
 414 (○), and crop yielding 10 t ha⁻¹ with a crop height of 1.0 m (◇) and 0.7 m (●), for different lodging return
 415 periods in the NWM environment. Dotted line indicates a NWM wheat crop with current average yield of 6
 416 t ha⁻¹ and putative minimum crop height compatible with this yield of 0.7 m

417 *Applicability of the lodging model*

418 The winter wheat lodging model has demonstrated significant accuracy to predict timing and amount of
 419 lodging (Berry et al. 2003b). However, its applicability for spring wheat has not been tested. The
 420 experiment of 2011 experienced enough natural lodging to test the lodging model developed for spring

421 wheat by comparing the severity of natural lodging against the predicted lodging risk calculated by the
 422 model. An index for natural lodging for each cultivar was calculated by summing the percentage of lodged
 423 area (recorded once or twice a week during the lodging period) between the first occurrence and harvest.
 424 The model predicted lodging susceptibility was calculated by inputting the values of the lodging-associated
 425 characters into the model and calculating the mean value of the stem and root failure wind speed which
 426 ranged 7.6 to 11.7 m s⁻¹. Lodging occurred during early to mid-grain filling on 35 cultivars whereas 28 were
 427 predicted by the model; lodging was absent in 25 genotypes and 12 were predicted by the model.
 428 Considering this, from the total of 60 cultivars the model correctly predicted 40 genotypes for either
 429 absence or presence of lodging giving a percentage of correct predictions of 67 %. Figure 8 is showing a
 430 reasonable correlation between observed and predicted rankings for cultivar lodging resistance.



431
 432 **Fig. 8** Predicted and experimental ranking of spring cultivars for lodging susceptibility under NWM
 433 environment during 2011. Ranking is in ascending order. (—) 1:1 line. Best fit line, $y = 0.60x + 6.52$;
 434 $R^2=0.35$ ($P < 0.001$)

435 **Discussion**

436 *Comparison of results with published literature*

437 Wind speed analysis for NWM environment has demonstrated that spring wheat growing in these
 438 conditions must withstand 22 m s⁻¹ and 18 m s⁻¹ to resist stem and root lodging, respectively. This indicates

439 that spring wheat will require stronger stems than UK winter wheat (18 m s^{-1} for stem and root lodging risk)
440 (Berry et al. 2007) and similar anchorage strength to support plants with the same height and yield and have
441 lodging only once in 25 years. However, several differences between spring and winter wheat types must
442 also be considered. It has been found that for a height at centre of gravity of 0.5 m spring wheat had a
443 greater natural frequency of 1.5 Hz compared with about 1.0 Hz for winter wheat (Berry et al., 2004).
444 Typical ear area for spring wheat averaged about 19 cm^2 compared with 12 cm^2 for winter wheat with
445 slightly greater yield and similar ears m^{-2} . It is likely that the absence of awns on UK winter wheat explains
446 at least part of this difference. Overall these differences mean that spring wheat will have a greater leverage
447 than winter wheat for crops with the same height, yield and ears m^{-2} (spring wheat = 383 N mm ; winter
448 wheat = 297 N mm).

449 Stem failure moment values for the bottom internode ranged from 134 to 252 N mm (Table 4). These
450 values are higher than the range of the stem failure moment measured in cultivar trials carried out on winter
451 wheat in the UK which ranged from 122 to 230 N mm (Berry et al 2003b; Berry et al 2007). This study has
452 shown a strong relationship between stem strength and structural stem biomass and between anchorage
453 strength and surface root biomass. If there is limited scope to reduce lodging risk by further shortening
454 crops then stem strength and anchorage strength will need to be increased, and this may have a substantial
455 biomass cost that will compete against grain yield formation. A previous study on winter wheat (Berry et al.
456 2007) estimated that a stem dry weight per unit length of 1.65 mg mm^{-1} was required to achieve a stem
457 strength of 100 N mm. However, the estimated biomass required for stem strength included both structural
458 and water soluble carbohydrate (WSC) and may therefore have over-estimated the amount of structural
459 stem biomass required for stem strength. In the present study, WSC content was not related to the stem
460 strength whereas structural biomass (composed mostly of lignin, cellulose and hemicellulose) was strongly
461 and positively associated with the stem strength. Knapp et al (1987) stated that lodging could be not related
462 to fluctuations in WSC and structural carbohydrates content. On the other hand, Ma (2009) found the wheat
463 gene TaCM (involved in lignin biosynthesis) was associated with stem strength and lodging index and
464 Wiersma et al (2011) found a positive association between lodging resistance and acid detergent lignin
465 (ADL) whilst Wang et al (2012) proposed that cellulose plays an important role in the ability of wheat
466 stems to resist lodging. There is therefore little evidence to suggest that WSC contributes to stem strength.
467 The present study measured that 1.13 mg mm^{-1} of structural biomass is required to achieve a stem strength
468 of 100 N mm. If it is assumed that spring and winter wheat have similar stem biomass/strength properties,

469 then this indicates that the study of Berry et al (2007) may have over-estimated the stem biomass required
470 to achieve specific strength targets by 40 – 50%.

471 Root biomass per plant in the top 10 cm of soil ranged from about 200 to 500 mg per plant and a root
472 plate spread of 30 to 55 mm. This is within a similar range to a study carried out in the UK which observed
473 a surface root biomass of 100 to 400 mg per plant and a root plate spread of 25 to 45 mm. Both studies had
474 similar plant populations of close to 160 – 180 plants m⁻². This study has shown that breeding for a wider
475 root plate will require greater investment in root biomass in the top 10 cm of soil. In order to increase root
476 plate spread by 10 mm an additional 263 mg of surface root biomass per plant was required. For the average
477 plant population (estimated at 163 plants m⁻²), this equates to an additional surface root biomass of
478 approximately 0.43 t ha⁻¹ to increase root plate spread by 10 mm. This compares with a winter wheat study
479 carried out in the UK which, for a single field experiment, estimated an additional 0.28 t ha⁻¹ of surface root
480 dry matter to increase the spread of the root plate by 10 mm (Berry et al., 2007). This comparison indicates
481 that spring wheat grown in NWM environment may require a greater investment in additional surface root
482 biomass to widen its root plate than winter wheat grown in the UK. This can be a consequence of
483 differences in specific root weight (dry weight per unit length) relating to ‘root thickness’ between UK
484 winter and NWM spring wheat (unfortunately not measured for the latter). Variation in root biomass has
485 been found to be a consequence of secondary thickening of the upper parts of roots (Berry et al., 2007).

486 *Implications of achieving a lodging-proof plant*

487 It has been estimated that to achieve a 1 in 25 year lodging return period for a typical spring wheat crop
488 grown in the NWM environment yielding 6 t ha⁻¹ (at 12% moisture) with a height of 0.7 m will require
489 approximately 3.93 t ha⁻¹ of structural stem biomass. Unpublished data from experiments described in this
490 study in 2011-13 shows that on average an additional 0.80 t ha⁻¹ of biomass is required for the leaf lamina
491 and sheath, and the chaff to grain dry weight ratio of 0.22 (Piñera-Chavez et al., 2016) gives a chaff dry
492 weight of 1.16 t ha⁻¹. This gives a total non-grain biomass of 5.89 t ha⁻¹. Straw yields of up to 6 t ha⁻¹ or just
493 over 6 t ha⁻¹ have been observed in NWM (Piñera-Chavez et al., 2016). This ideotype would require a
494 surface root biomass of approximately 1.10 t ha⁻¹ which was not been achieved by any cultivar in this study.
495 It therefore appears that for this ideotype it should be possible to achieve stem biomass requirements but not
496 root biomass requirements with current germplasm. The NWM environment can support greater yield than
497 the average 6 t ha⁻¹ currently achieved and could be up to 9 t ha⁻¹ (Fischer and Edmeades, 2010). It is
498 estimated that cultivars yielding 10 t ha⁻¹ (with a height of 0.7 m) will require greater above-ground non-

499 grain biomass equating to 4.67 t ha^{-1} (assuming no change in leaf and leaf sheath) and 1.28 t ha^{-1} of surface
500 root biomass to achieve a lodging return period of 25 years. It should further be recognised that the
501 breeding program at CIMMYT has increased the plant height of wheat to 1.0 m or above in the period of
502 1966 to 2009 (Aisawi et al. 2015), where the raised bed planting system may favour taller crops better at
503 capturing the light in the gaps between the beds early in the season (Fischer et al. 2005). In the UK, Berry et
504 al (2014) has shown that breeders have not shortened varieties since the 1990s. This indicates that achieving
505 a high yield and a short (0.7 m tall) crop may be challenging. If a yield of 10 t ha^{-1} can only be achieved
506 with a 1.0 m tall crop, then the above-ground non-grain biomass requirement increases to 10.1 t ha^{-1} and the
507 surface root biomass to 1.68 t ha^{-1} . These biomass requirements will be very challenging to meet and
508 illustrate that breeders must breed not only for greater total biomass, but also this biomass must be
509 optimised carefully to maximise strength per unit of biomass. Certainly, it will be possible to increase total
510 biomass as shown in the UK (Shearman et al., 2005) and in NWM (Aisawi et al. 2015). Recently, several
511 studies have identified QTLs that could be used to increase both yield and straw biomass (above-ground
512 biomass) in wheat (Berry et al., 2008; Li et al., 2014; Xu et al., 2014). Other cereals such as rice have also
513 shown QTLs related to both yield and straw biomass (Suji et al., 2012). Optimising how the additional dry
514 matter is partitioned to maximise its usefulness will be very important. Targets for improving the efficiency
515 with which non-grain biomass is used include; maximising stem strength per unit of stem biomass,
516 maximising grain weight to ear weight ratio, minimising the production of infertile tillers and achieving
517 high yields with shorter crops. Breeding for wider stems seems to be the most efficient way to increase the
518 stem strength which together with a reduced leverage given by a shorter plant represents a strategic option
519 to minimise structural biomass requirements. Additionally, breeding for more compact ears (unawned) in
520 spring wheat could further reduce this leverage and consequently reducing more the biomass requirements.
521 However, careful must be taken because awned ears have been related to drought and heat resistance
522 (Blum, 1986).

523 Dry matter harvest indices for these lodging proof ideotypes equate to 0.46 for a 0.7 m tall crop yielding
524 6 t ha^{-1} , 0.54 for a 0.7 m tall crop yielding 10 t ha^{-1} and 0.41 for a 1.0 m tall crop yielding 10 t ha^{-1} . These
525 figures are some way below the estimated potential harvest index for wheat of 0.62 (Austin, 1980). Winter
526 wheat grown in the UK with a yield of 8 t ha^{-1} and height of 0.7 m was estimated to have a harvest index of
527 0.42 (Berry et al., 2007). However, it is likely that this study over-estimated the stem biomass requirement
528 by including water soluble stem carbohydrate in the stem biomass measurements. If the same relationship

529 between stem failure and structural stem weight observed for this present study for spring wheat is used for
530 winter wheat, and a leaf and leaf sheath biomass of 1.0 t ha^{-1} is included, then this gives a harvest index of
531 0.49. The relatively high levels of non-grain biomass and low harvest indices that are estimated to result
532 from breeding crops with a lodging return period of 25 years suggest that the high investment in non-grain
533 biomass may compete with yield formation and limit the rate of breeding improvement in grain yield. This
534 potential trade-off arises from the overlapping of the development periods of lodging traits and key yield-
535 determining processes such as floret development and production of water soluble reserves. In fact, Slafer
536 and Rawson (1994) stated that all the processes included from GS30 to GS60 (Zadoks et al., 1974) are
537 considered of major importance for yield construction. Crook et al. (1994) described the development of the
538 lodging characters (stem and root strength) from tillering (GS20) until maturity (GS87) and concluded that
539 these traits ceased develop soon after anthesis (GS65). There may be a net yield benefit from accepting a
540 shorter lodging return period, since the advantage of lower non-grain biomass investment on yield potential
541 may outweigh yield losses from more frequent lodging. If the lodging return period is reduced from 25
542 years to 10 years then the harvest index increases from 0.46 to 0.51 for a crop yielding 6 t ha^{-1} with height
543 of 0.7 m, increases from 0.54 to 0.58 for a 0.7 m tall crop yielding 10 t ha^{-1} , and increases from 0.41 to 0.46
544 for a 1.0 m tall crop yielding 10 t ha^{-1} .

545 This paper showed a significant effect of the leaf sheath on the stem strength measured 20 days after
546 GS65 on internodes 2 to 5 (peduncle) where the presence of the leaf sheath increased stem strength by 12%
547 for internode 2 to an increase of 34% on the peduncle. The effect on internode 1 was not significant because
548 the leaf sheath was mostly senesced or not present at GS65 + 20 d. The leaf sheath has been reported to
549 have an important mechanical role ensuring the plant standing ability in other species including;
550 *Arundinaria tecta* (Poaceae) (Niklas, 1998), *Poa araratica*, *Bromus erectus*, *Arrhenatherum elatius*
551 (Poaceae), *Luzula nivea* (Juncaceae), *Carex arctata* (Cyperaceae) (Kempe et al. 2013) and *Triticale*
552 (Zebrowski, 1992). These findings indicate that leaf sheath is a mechanical component of the stem
553 especially soon after flowering, however, its effects will diminish as the crop matures as the leaf sheath
554 dries and eventually falls off. This study has estimated the structural requirements to avoid lodging for a
555 plant at harvest without leaf-sheaths surrounding the internodes. This approach is appropriate for plants at
556 harvest and is likely to be appropriate during a few weeks prior to harvest for the lower internodes, which
557 most commonly buckle, and whose leaf-sheaths senesce first. However, it will probably over-estimate the
558 stem strength required to avoid lodging at earlier growth stages (e.g. at flowering) because the contribution

559 of the leaf sheath is not included. Further work is required to quantify how the contribution of the leaf-
 560 sheath to the strength of each internode diminishes as the plant develops so that the minimum strength of
 561 the true stem required for various lodging return periods can be modelled more accurately.

562 NWM spring wheat lodging ideotype trait values for a typical yield crop with a 25 year return period
 563 differ from the equivalent UK winter wheat lodging ideotype values as follows; spring wheat requires a
 564 10% smaller root plate and a 7% stronger stem strength. Rainfall is practically absent during the lodging
 565 risk period in the NWM environment and water supply has to be provided by periodic irrigation. This
 566 condition reduces the root lodging risk period to 10 days of grain filling period which, in turn, reduces the
 567 maximum wind gust speed required to withstand root lodging. Drier, but windier, conditions in NWM
 568 compared with the UK mean that both spring and winter wheat ideotypes must withstand the same
 569 maximum wind gust speed (18 m s^{-1}) for a 25-year root lodging return period; however, yield of 8 t ha^{-1} for
 570 the UK ideotype compared with 6 t ha^{-1} for NWM contribute to the greater root plate spread required by the
 571 UK ideotype. The greater stem strength requirement for spring wheat is mainly due to a higher maximum
 572 wind gust speed on the NWM environment (22 m s^{-1}) and the greater ear area of spring wheat.

573 The genetic ranges for the key lodging traits are described in Table 4 and in companion paper (Piñera-
 574 Chavez et al., 2016). This shows that it should be possible for plant breeders to achieve some of the
 575 ideotype dimensions for a spring wheat crop yielding 6 t ha^{-1} with height of 0.7 m. Nevertheless, if it is
 576 assumed that yield will increase in the following decades then the biophysical targets will increase. For
 577 example, if yield is increased to 10 t ha^{-1} then the stem diameter will increase by 8%, root plate spread by
 578 6% and stem strength by 18%. In this case it would be unlikely that plant breeders could achieve a lodging
 579 proof plant with a lodging return period of 25 years with current germplasm. Our analysis also showed that
 580 the target dimensions will be further increased if yield improvements must also be accompanied by crop
 581 heights of more than 0.7 m.

582 **Table 4** Spring wheat genotypic range for the lodging key traits (Piñera-Chavez et al., 2016)

Trait	Genetic range
Diameter (mm)	3.35 – 4.47
Wall width (mm)	0.64 – 0.92
Internode failure moment (stem strength) (N mm)	134 – 252
Material strength (MPa)	27.4 – 59.4
Root plate spread (mm)	34 – 42
Height (m)	0.73 – 1.07

583 *Lodging probability of 1 in 25 years, 200 plants m^{-2} , 500 shoots m^{-2} and grain yield of 6 t ha^{-1}

584 **Conclusion**

585 Testing of an adapted lodging model for elite spring wheat lines showed it to be useful tool for ranking the
586 susceptibility to lodging of cultivars under crop, soil and weather conditions in NWM. This has enabled the
587 calculation of the target lodging resistance traits of the lodging resistant ideotype for this particular
588 environment. A positive stem and root biomass correlation with the stem strength (internode failure
589 moment) and anchorage strength (root plate spread) was identified which enabled the structural dry matter
590 requirements to be calculated for lodging proofness. It has been established that any improvement to
591 achieve a lodging-proof crop that lodges only once in a period of 25 years would require an increase in the
592 stem biomass which in turn could imply a trade-off with grain yield if improvement of the latter depends
593 solely on increasing the HI. Alternatively, decreasing of the proportion of straw biomass to the total above-
594 ground dry matter would increase the risk of lodging unless more total biomass is made available to straw
595 through increasing RUE. This study therefore indicates that for plant breeders to achieve both high yields
596 and lodging proofness they must either breed for greater total biomass or develop high yielding germplasm
597 from shorter crops of 0.7 m or less.

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776 **Supplementary material**777 **Table S1** The CIMMYT Mexico Core Germplasm Panel (CIMCOG), consisting of 58 *T. aestivum* and two
778 *T. durum* cultivars

No.	NAME	Year of evaluation*
1	ATTILA (PBW 343)	2011
2	ATTILA*2/PBW65	2011
3	ATTILA*2/PBW65*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES	2011
4	ATTILA//PGO/SERI/3/PASTOR	2011, 12
5	BABAX/LR42//BABAX/3/ER2000	2011
6	BABAX/LR42//BABAX/3/VORB	2011, 12, 13
7	BACANORA T 88	2011, 12, 13, 14
8	BAVIACORA M 92	2011
9	BCN/RIALTO	2011, 12, 13
10	BCN/WBLL1	2011
11	BECARD (Wbll 1*2/Kiritati)	2011, 13
12	BECARD/5/KAUZ//ALTAR 84/AOS/3/MILAN/KAUZ/4/HUITES	2011, 12, 13
13	BRBT1*2/KIRITATI (HIST 14)	2011, 12, 13
14	C80.1/3*BATAVIA//2*WBLL1/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA(213)//PGO/4/HUITES	2011
15	CAL/NH//H567.71/3/SERI/4/CAL/NH//H567.71/5/2*KAUZ/6/PASTOR/7/CROC_1/AE.SQUARROSA (205)//KAUZ/3/ATTILA/8/CAL/NH//H567.71/3/SERI/4/CAL/NH//H567.71/5/2*KAUZ/6/PASTOR	2011, 12, 13
16	CAL/NH//H567.71/3/SERI/4/CAL/NH//H567.71/5/2*KAUZ/6/PASTOR/7/WHEAR/8/CAL/NH//H567.71/3/SERI/4/CAL/NH//H567.71/5/2*KAUZ/6/PASTOR	2011, 12, 13
17	CHIR3/4/SIREN//ALTAR 84/AE.SQUARROSA (205)/3/3*BUC/5/PFAU/WEAVER	2011
18	CHWL86/6/FILIN/IRENA/5/CNDO/R143//ENTE/MEXI_2/3/AEGILOPSSQUARROSA(TAUS)/4/WEAVER	2011
19	CMH79A.955/4/AGA/3/4*SN64/CON67//INIA66/5/NAC/6/RIALTO	2011, 12, 13, 14
20	CIRNO (SOOTY_9/RASCON_37//CAMAYO)	2011, 12, 13
21	CNDO/R143//ENTE/MEXI_2/3/AEGILOPSSQUARROSA(TAUS)/4/OCI/5/PASTOR/6/TEMPORALRAM87/ROMO96	2011
22	CNDO/R143//ENTE/MEXI_2/3/AEGILOPSSQUARROSA (TAUS)/4/WEAVER/5/2*KAUZ	2011
23	CNO79//PF70354/MUS/3/PASTOR/4/BAV92*2/5/FH6-1-7	2011, 12, 13
24	CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2	2011, 12, 13, 14
25	GK ARON/AG SECO 7846//2180/4/2*MILAN/KAUZ//PRINIA/3/BAV92	2011
26	KBIRD//INQALAB 91*2/TUKURU	2011, 12, 13
27	KFA/3/PFAU/WEAVER//BRAMBLING/4/PFAU/WEAVER*2//BRAMBLING	2011, 13
28	MEX94.27.1.20/3/SOKOLL//ATTILA/3*BCN	2011
29	MILAN/KAUZ//PRINIA/3/BAV92	2011, 12, 13
30	MUNAL #1	2011
31	Navoja M2007 (=ATTILA/PASTOR)(Hist 10)	2011
32	OASIS/5*BORL95/5/CNDO/R143//ENTE/MEXI75/3/AE.SQ/4/2*OCI	2011, 12
33	OASIS/KAUZ//4*BCN/3/2*PASTOR (= Misr#1 in Egypt)	2011
34	OASIS/KAUZ//4*BCN/3/2*PASTOR/5/FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/7/CAL/NH//H567.71/3/SE RI/4/CAL/NH//H567.71/5/2*KAUZ/6/PASTOR	2011
35	PANDORA//WBLL1*2/BRAMBLING	2011
36	PASTOR/3/URES/JUN//KAUZ/4/WBLL1	2011
37	PAVON F 76	2011, 12, 13
38	PBW343*2/KUKUNA*2//FRTL/PIFED	2011, 12, 13
39	PFAU/SERI.1B//AMAD/3/WAXWING (=Super 152)	2011, 12, 13
40	ARMENT//2*SOOTY_9/RASCON_37/4/CNDO/PRIMADUR//HAI-OU_17/3/SNITAN	2011
41	QUAIU #3//MILAN/AMSEL	2011
42	RL6043/4*NAC//2*PASTOR (WAMI 249)	2011
43	ROLF07*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES	2011
44	SERI M 82 (Hist 3)	2011, 12, 13
45	SIETE CERROS T66 (Hist 1)	2011, 12, 13
46	SOKOLL*2/3/BABAX/LR42//BABAX	2011
47	SOKOLL//PBW343*2/KUKUNA/3/ATTILA/PASTOR	2011, 12, 13
48	TACUPETOF2001/7/CAL/NH//H567.71/3/SERI/4/CAL/NH//H567.71/5/2*KAUZ/6/PASTOR/8/BABAX/LR42//BABAX* 2/3/KURUKU	2011, 12, 13
49	TACUPETO F2001/BRAMBLING*2/5/KAUZ//ALTAR 84/AOS/3/MILAN/KAUZ/4/HUITES	2011, 12, 13
50	TC870344/GUI/TEMPORALERA M 87/AGR/3/2*WBLL1	2011, 12, 13
51	TRAP#1/BOW/3/VEE/PJN//2*TUI/4/BAV92/RAYON/5/KAUZ//ALTAR 84/AOS/3/MILAN/KAUZ/4/HUITES	2011, 12, 13
52	TRCH/SRTU/5/KAUZ//ALTAR 84/AOS/3/MILAN/KAUZ/4/HUITES	2011
53	UP2338*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/MILAN/KAUZ//CHIL/CHUM18/6/UP2338*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ	2011, 12, 13
54	W15.92/4/PASTOR//HXL7573/2*BAU/3/WBLL1	2011

55	WBL1*2/KIRITATI (BECARD)	2011, 12, 13
56	WBL1*2/4/BABAX/LR42//BABAX/3/BABAX/LR42//BABAX	2011, 13
57	WBL1*2/KURUKU*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES	2011, 12, 13, 14
58	WBL1*2/TUKURU*2/4/CROC_1/AE.SQUARROSA (205)//BORL95/3/2*MILAN	2011
59	WHEAR/SOKOLL	2011, 12
60	YAV_3/SCO//JO69/CRA/3/YAV79/4/AE.SQUARROSA(498)/5/LINE1073/6/KAUZ*2/4/CAR//KAL/BB/3/NAC/5/KAUZ /7/KRONSTAD F2004/8/KAUZ/PASTOR//PBW343	2011, 12, 13, 14

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*Indicated the year of the growing season were the cultivar was evaluated

Table S2 Lodging measurement methods

Type of character	Description
Root characters	Crown roots were identified by their inherent rigidity and the tendency for soil particles to adhere to their dense covering of root hairs, or rhizosheath. This distinguishes them from seminal roots, which number six or less, emerge directly from the seed with less rigidity, and usually have no adhering soil. The rhizosheath section of a crown root is termed the 'rigid root length', and there is usually little variation between the roots of individual plants. However, some plants had very variable rigid root lengths, so that determination of the spread of the root plate and its depth was more subjective. The point at which the majority of rigid root portions terminated was estimated visually to define 'root plate spread'. Both the maximum root plate spread and the root plate spread at 90° to the maximum (usually the smallest spread) were measured. Structural rooting depth was measured as the distance from base of the root plate to the soil surface, identified as the point where stem colour changes from white to green. Root plate spread was determined from an average of the maximum and minimum root plate spread.
Leverage characters (main shoot)	Natural frequency was measured in the field on a still day. After selection of plants, the main shoot was identified (the tallest with the largest ear) and isolated from any neighbouring shoots. The shoot was pulled back (at the collar of the ear) 5-10 cm from the vertical and released. The time required for three complete oscillations in the line of displacement was registered and the number of oscillations recorded. Natural frequency was then calculated by dividing the number of oscillations during the timed period, by the length of the time period (s). Other measurements included the number of fertile shoots per plant (shoots with ears), plant height to the ear tip, and area of each main shoot ear assessed with a LI-3100C area meter (LI-COR®)

	<p>during 2011-12 and 2012-13. Height at the centre of gravity of the main shoot was determined by balancing the main shoot without roots on ruler with leaves and ear still attached and recording the distance from the point of balance to the base of the stem.</p>
<p>Stem characters</p>	<p>Stem measurements were only done on the main shoot. Firstly, internode one was identified, defined as the first internode of more than 10 mm, originating at or just below the ground surface and without crown roots emerging from its upper node. Subsequent internodes ascending the stem were numbered two, three, four etc., with the uppermost internode referred to as the peduncle. Measurements of the stem base were carried out on internodes one and two of each main shoot, and the lengths of these internodes were measured from the mid-point of their adjacent nodes. Stem diameter was measured at the middle of each internode using digital callipers. The breaking strength of internodes one and two was also determined using a three-point bending test (Easson et al., 1992; Graham, 1983); nodes adjacent to the internode were supported on the 'Y' frame, which was clamped to the bench before the hook of a Mecmessin[®] basic force gauge (200 N x 0.05 N) was placed around the mid-point of the internode and a pulling pressure applied at an even rate. The force just before the internode bending was considered its breaking strength. Finally, the stem wall width was measured by cutting internodes one and two at their mid-point. Once those internodes were cut, two measurements at right angles to each other were recorded and averaged.</p>