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

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Abstract

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

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

Introduction

Lodging is defined as the permanent displacement of plant stems from their vertical position as a result of wind acting on the shoot and rain or irrigation weakening the soil and reducing anchorage strength (Berry et al. 2004). Lodging grain yield reductions of wheat can be in the range of 7 to 80% (Acreche and Slafer, 2011; Berry and Spink, 2012; Easson et al., 1993; Fischer and Stapper, 1987; Tripathi et al., 2005; Weibel and Pendleton, 1964) and commonly are accompanied by reductions of bread making quality (Berry et al. 2004). In fact, as Pinthus, (1974) indicated, these reductions can be at least as great as that resulting from crypotogamic diseases and insect pests in high yielding environments. Lodging affects all cereal species and many other crops, such as oilseed rape and sunflowers, throughout the world. In wheat, lodging can increase susceptibility to pests and diseases (Berry et al., 2004; Pinthus, 1974), induce negative effects on crop development (decreasing grain per m^2 and average grain weight) (Acreche and Slafer, 2011; Fischer and Stapper, 1987) and complicate harvest (Berry et al., 2004; Fischer and Stapper, 1987; Pinthus, 1974). Widespread lodging affects from 15 to 20% of the UK wheat growing area once every three or four years

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

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

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

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

Baker et al. (1998) developed a model of lodging that has been validated by Berry et al. (2003b) for winter wheat in the UK. The model was based on the interaction of plant, soil and wind characteristics and calculates the stem and root lodging risk according to the wind speed required to over-turn the root anchorage system or to buckle the stem base of a plant. A preliminary attempt to quantify the stem strength and anchorage strength required by winter wheat to withstand 1 in 25 year wind gusts in the UK has been made by Berry et al. (2007) using this lodging model. This indicated that substantial amounts of dry matter may need to be invested in the stem and anchorage system to make plants lodging-proof for a period of 25 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 first top 10 cm of soil) (Foulkes et al. 2011). This would mean that the maximum harvest index (ratio of 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, rising to 0.50 for a crop yielding 16 t ha^{-1}, which is significantly less than the theoretical maximum harvest index 0.62 estimated by Austin, (1980). Additionally it is possible that the investment in dry matter for the stem and anchorage system during stem elongation which is the critical phase for determination of grain number (Fischer, 1985) may compete for resources with grain yield determination. The implications of Berry et al. (2007) are that the dual requirements of breeding for greater yield and greater lodging resistance will be challenging. However, parts of the analysis were based on limited datasets for winter wheat and it was not possible to distinguish between the structural dry matter and water soluble carbohydrate in the stem, which may mean that the estimate of stem structural dry matter to avoid lodging was over-estimated.

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

Experimental methods

Experiments

Four field experiments were established during the field seasons 2010-2011, 2011-2012, 2012-2013 and 2013-2014 (referred to hereafter as 2011, 2012, 2013 and 2014, respectively) in the experimental station of CENEB (Campo Experimental Norman E. Borlaug) located in the Valle del Yaqui, Sonora, Mexico (27.9°N and longitude 109.9°W). The soil type at the experimental station is a coarse, sandy clay, mixed montmorillonitic typic caliciorthid, slightly alkaline (pH 7.7) in nature (Sayre et al. 1997), bulk density of 1.32 g cm^{-3} and organic matter of 0.7 % approximately (CIMMYT internal records). Detailed information about experiments and cultivars (CIMMYT Mexico Core Germplasm Panel or CIMCOG consisting of 58 *T. aestivum* and two *T. durum and* described in Table S1) is given in a companion paper by (Piñera-Chavez et al., (2016). The whole CIMCOG panel was established during 2011 and a subset of 30 cultivars were used for 2012 and 2013 (as indicated in Table S1). Experiments were managed under a conventional agricultural management but maintaining yield potential conditions. The average seed rate for all plots in experiments 2011, 2012 and 2013 was 10.6 g m^{-2} which gave a range 213-292 seeds m^{-2}. For the experiment in 2014 a subset of five cultivars with contrasting values for stem strength, anchorage strength and stem wall material strength (cultivars 7, 19, 24, 57 and 60, see Table S1) was established using seed rates of 75, 125 and 175 seeds m^{-2} to evaluate the effect of low plant populations on lodging traits. The irrigation schedule included five to six flood irrigation events (including one at sowing) during the cycle and the fertilization was 200 kg ha^{-1} of N (25 % before sowing and 75 % before first irrigation event) and 50 kg ha^{-1} of P (before sowing). Plant growth regulators were not applied in any of the experiments. Plant emergence dates (at 50 % of plants emerged) were recorded at 15 of December 2010, 16 of December 2011, 02 of December 2012 and 01 of December 2013 for experiments 2011, 2012, 2013 and 2014, respectively.

Measurements

Plant measurements were done at GS65 + 20 days (Zadoks et al. 1974) during 2011, 2012 and 2013 as was described in (Piñera-Chavez et al., 2016) (detailed key information of measurements is given in Table S2). Additionally, during 2013 and 2014 main shoot measurements of the length and breaking strength following removal of the leaf-sheath of the internodes 1 to 5 were determined for five cultivars with contrasting performances in stem strength, material strength and anchorage strength (Table 1). Internode 1 in the main shoot 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. Also, dry weight and the following determination of the water soluble carbohydrates content (WSC) was made on these internodes. WSC content was also determined for the whole main shoot in all cultivars used for experiments 2011, 2012 and 2013. These analyses were carried out in the Maize Nutrition Quality and Plant Tissue Analysis Laboratory from CIMMYT (El Batan, Mexico) using the Anthrone method (Galicia et al. 2008).

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/BB/3/NAC/5/KAUZ/7/KRONSTAD F2004/8/KAUZ/PASTOR//PBW343 [a]	Lowest material strength

Calculations

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

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

$$B_s = \frac{1}{4} F_s h \tag{1}$$

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

$$B_R = k_3 s d^3 \tag{2}$$

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

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

Natural frequency is considered a parameter of major importance of the wind-induced leverage (base bending moment) (Baker et al., 1998), although, height at centre of gravity and ear projected area have also a great influence (Berry et al., 2003b). Assuming the wind-induced leverage decreases linearly for progressively higher positions up the stem (Berry et al. 2006), bending moment at the base of subsequent internodes 2 to 5 was calculated by multiplying the leverage exerted at the base of internode 1 with the ratio of the distance between the base of internodes 2, 3, 4 or 5 and the mid-point of the ear with the total stem height at the mid-point of the ear (Berry et al. 2007). These ratios were measured in spring wheat at 0.84 for 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-point of the length internode 5 or peduncle was used to calculate the bending moment (19%) due to non-uniform geometric properties (Berry et al. 2007). This means that the leverage exerted at the base of internodes 2, 3, 4 and the peduncle should be 84, 70, 50 and 19 %, respectively, of the leverage exerted at the base of internode 1.

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

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

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

Statistical analysis

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

Wind speed characterisation

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

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

where σ/U_m is the turbulence intensity (TI). A value of $\sigma/U_m = 0.5$ was used, again following the work of Berry et al. (2003b) who used the value determined by Finnigan (1979) for wind over a wheat crop. These values were then corrected for differences in the roughness, z_0, at the airport weather stations and the crop locations, and also for the difference in height above ground, z, of the airport anemometers (10 m), the met station anemometer (1.5 m) and the pertinent wind speed height for crop lodging of 2 m (Baker et al. 1998; Berry et al. 2003b). This correction takes the form:

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

where subscripts *c* and *w* refer to the crop and weather station locations, respectively. z_0 over the crops has 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 $z_0 = 0.01$ m at the weather station (Berry et al. 2003b). Finally, an altitude correction has been applied to the gust wind speed using the V_{99} correction factor of $(1 + 0.009h)$ specified in Baker et al. (1998). The 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 altitudes respectively. As stated in Berry et al. (2003b), these methods were developed based on UK Meteorological Office data and should therefore be applied with care in other locations. In particular, these methods are only applicable where synoptic (non-convective) winds are expected.

In order to allow the analysis to concentrate on the period when lodging risk is possible, the hourly gust values were split by month (i.e. 12 groups of data were formed from the 40 years of data, each corresponding to a particular month). The probability of the gust speed exceeding a certain value was calculated for each month on a per day basis. At each scale, probabilities of the gust speed being within a certain range were calculated by sorting the values into 0.5 m s^{-1} wide “bins”, with the probability of gusts within the range covered by each bin calculated simply from the number of values in that bin divided by the total number of values. Probabilities of exceeding a certain value were calculated as the sum of the probabilities for the bins whose ranges exceeded the required value. The probability of experiencing any particular wind gust during the lodging risk period was then calculated using daily gust speed probabilities for the months during which lodging is possible and assuming a stem lodging risk period of 50 days in March and April (assuming one wheat cycle per year) (window between cultivars with earliest flowering and the latest maturity was 52 days). Root lodging risk increases when the soil surface is wet (Easson et al. 1995; Berry et al. 2003a), typically when the first 50 mm of soil is at field capacity (Baker et al. 1998). This can be attributed to the movement of the plant crown in a saturated soil surface after flood irrigation in irrigated environments (Fischer and Stapper, 1987) or after precipitation in rainfed environments (Crook and Ennos, 1994), Moreover, Sterling et al. (2003), using a portable wind tunnel in the field, found that root lodging occurred only when the soil was saturated. Additionally, it is well known that water supply most spring wheat worldwide is given by flood irrigation in flat beds. It therefore seems sensible to consider the root lodging risk when the soil surface is moist. For our purposes, we estimated the root lodging risk period for the NWM environment to be 10 days, based on the number of days when the first 60 mm of soil depth (maximum root plate depth exceeded 50 mm in CIMCOG panel) was at 50% of plant available water during the 50 day lodging risk period. At lower soil moisture content, the soil is usually too strong to permit root lodging. Spring wheat in this region typically receives three flood irrigation events during the 50 day lodging risk period, each delivering approximately 73 mm water (0 – 120 cm soil core depth). Windy conditions often occur post-anthesis which may coincide with irrigations indeed in that period in 2014 and 2016 windstorms affected the area. Farmers pay special attention whether to apply the last irrigation or not (normally at mid grain filling) because of the intensity of the windy season. This is a difficult decision to make because avoiding the last irrigation sometimes ends in grain yield losses. Using internal records of field capacity and permanent wilting point from CENEB and evapotranspiration data from nearest weather station it has been estimated that the top 150 mm of soil dries to 50 % of plant available water after 8 days of irrigation. The soil tends to dry from the top downwards which indicates that the top 60 mm of soil will be dried to 50% plant available water within about 3.2 days, giving about 10 days when the top 60 mm of soil may be moist and weak enough to permit root lodging. A review of rainfall data over the past 40 years showed that the chance of more than 10 mm of rain (enough to bring the top 60 mm of soil to field capacity) falling in one day during March or April was very small.

Lodging model development

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

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

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

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

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

$$S_L = h - E_L$$

(11)

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

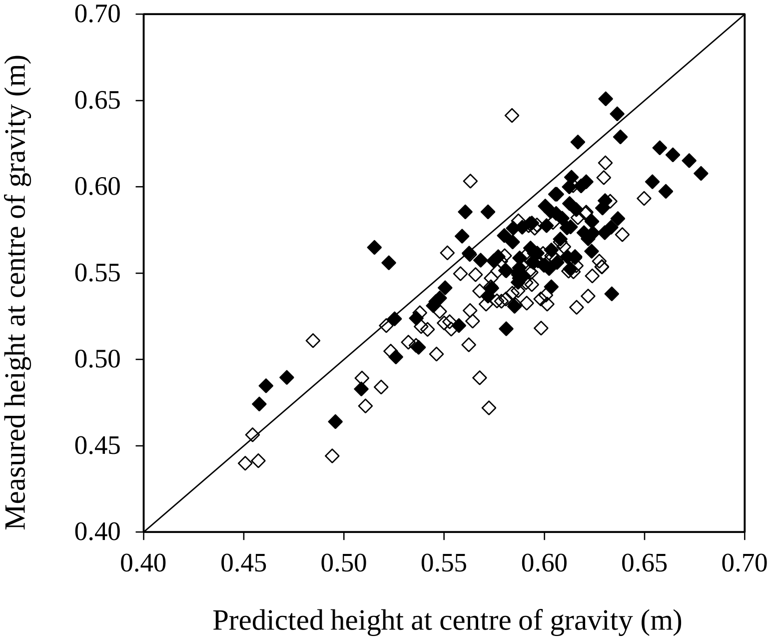

Fig. 1 Predicted and measured height at centre of gravity at GS65 + 7 days and GS65 + 20, respectively, for plot means of 2012 (closed squares) and 2013 (open squares). (—) 1:1 line. Best fit line, y = 0.70x + 0.15; R^2=0.64 (P < 0.001)

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

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

(12)

$$A = 9.95 + 1.02E_W \tag{13}$$

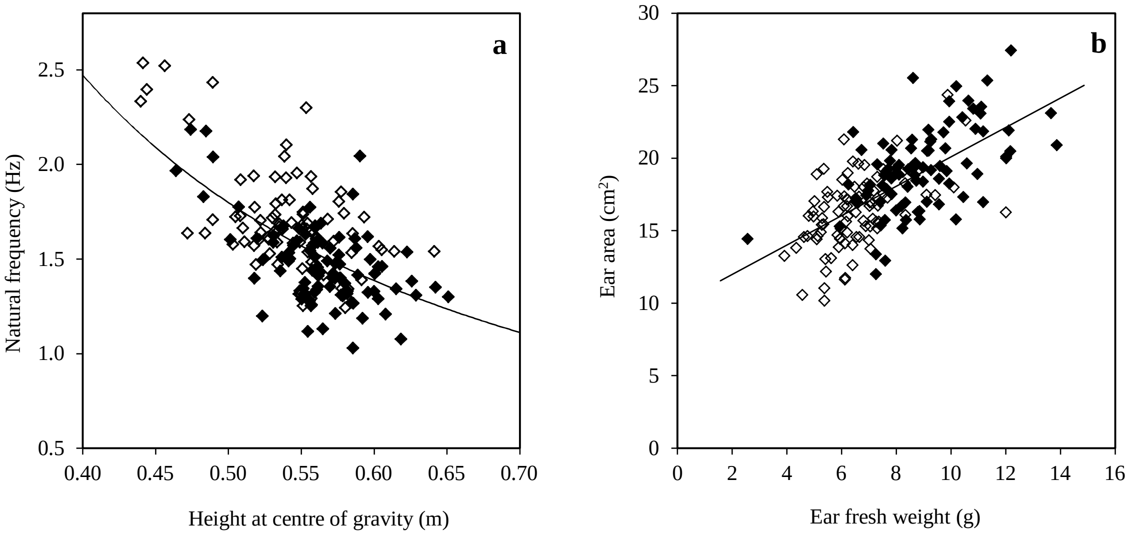

Fig. 2 (a) Height at centre of gravity at GS65 + 20 plotted against natural frequency for plot means of 2012 (closed squares) and 2013 (open squares). Regression line: $y = 0.67x^{-1.4}$ ($R^2=0.38$; $P < 0.001$). (b) Ear fresh weight plotted against ear area at GS65 + 20, for plot means of 2012 (closed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

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

Results

Wind gust speed probabilities

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

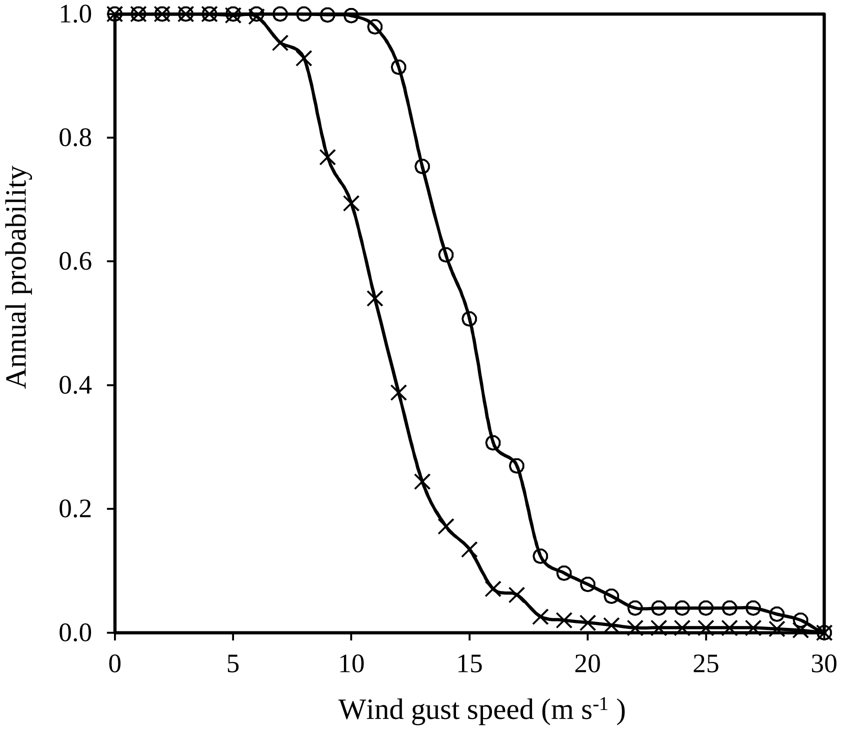

Fig. 3 North-West Mexico seasonal maximum wind gust probabilities for 50 days of high stem lodging risk (○) and for 10 days of high root lodging risk (when surface soil horizon is moist) (×)

Annual wind gust speed return periods for the NWM environment (Table 2) show that the plant must withstand a wind gust of 22 m s^{-1} to have a stem lodging return period of 25 years, and it must withstand a 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 critical wind speeds that must be withstood fall to 19 m s^{-1} and 16 m s^{-1} for stem and root lodging, respectively. Considering lodging return period as the period of time between lodging events or the period 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 lodging return period of 25 years (comparable with the UK lodging resistant ideotype). Berry et al., (2004) defined lodging proofness as: "*the structure that can withstand the strongest wind likely to occur over a cereal crop once every generation*".

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

25	22	18

Calculating the lodging-proof ideotype

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

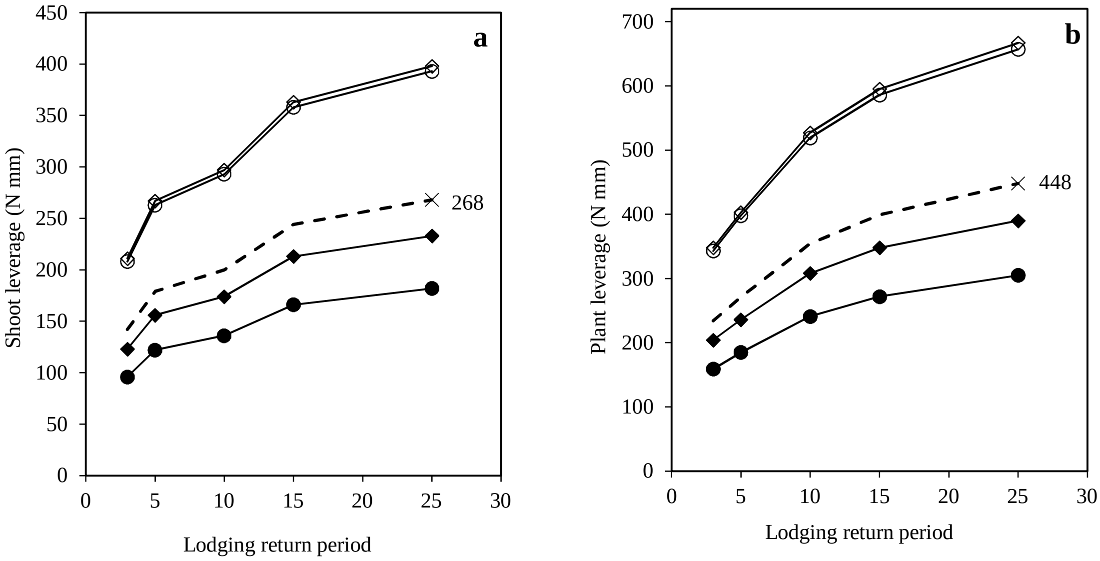

Fig. 4 Shoot leverage (a) and plant leverage (b) for a crop yielding 6 t ha^{-1} with a crop height of 1.0 m (○) and 0.5 m (●), and crop yielding 16 t ha^{-1} (◊) and 4 t ha-1 (♦) with a crop height of 0.7, for different lodging

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

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

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

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 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 25 years. These calculations assumed the soil was rolled after sowing to consolidate it. A 0.7 m tall crop yielding 6 t ha^{-1} with a lodging return period of 5 years would require a stem diameter of 4.04 mm with a material strength of 35 MPa or alternatively the required strength could be achieved with a stem diameter of 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 period of 25 years would require a stem diameter of 6.09 mm with a material strength of 35 MPa or 5.24 mm with a material strength of 50 MPa (Table 3).

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

[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

Biomass and failure moment of stem and anchorage system

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

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

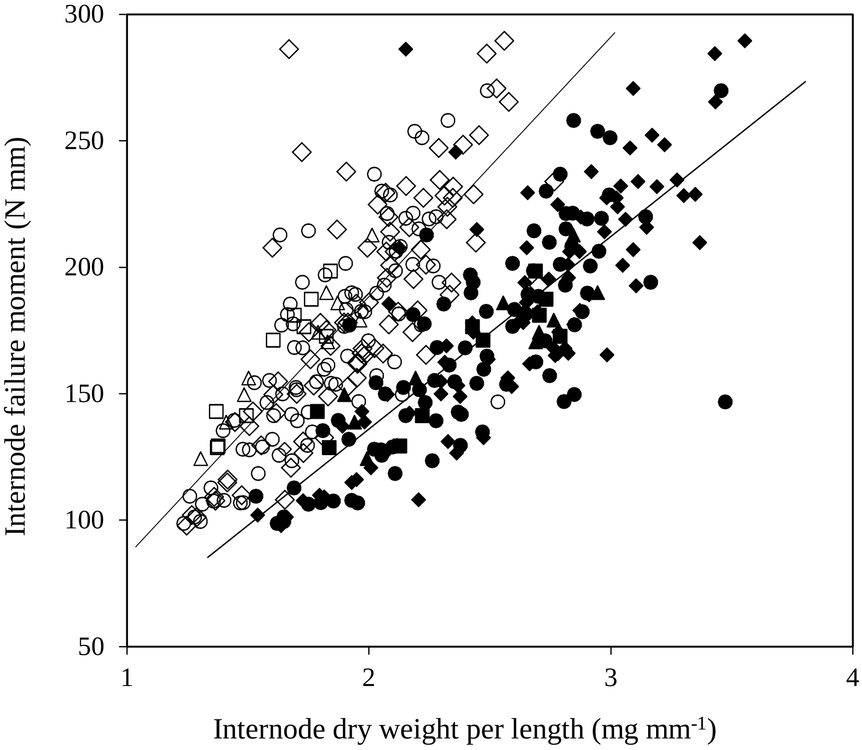

Fig. 5 Dry weight per unit length plotted against internode failure moment of internode 1 (diamonds), internode 2 (circles) for 27 genotypes (2011, 2012 and 2013 experiments) and of internodes 1, internode 2, internode 3 (triangles) and internode 4 (squares) for five genotypes (2013 and 2014 experiments).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

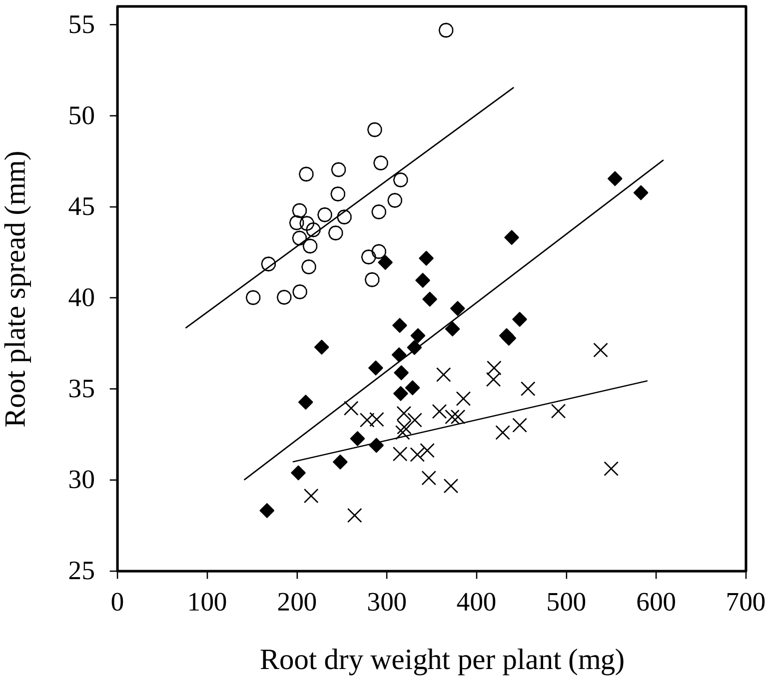

Fig. 6 Surface root dry weight per plant plotted against root plate spread of 27 spring wheat genotypes. Parallel model for (♦) 2012 experiment (y = 0.038x + 24.7) and (○) 2013 experiment (y = 0.038x + 35.6); $R^2 = 0.74$; P < 0.001). Expreiment (×) 2011 showed a regression line of y = 0.011x + 28.8 with an R^2 of 0.18 ($P < 0.05$)

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

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

The amount of structural stem and surface root dry matter required to resist lodging for a range of crop types and lodging return periods are described in Fig. 7. The structural stem biomass required to achieve specified lodging return periods was first estimated for each individual internode using the empirical equation $y = 103x – 16.8$ from Fig. 6 for 2011-14 data, where the "*y*" value was the leverage exerted at the base of each internode and the “x” value was the structural dry weight per unit length. The structural dry weight of each internode was calculated by multiplying the dry weight per unit length by the internode length. The structural dry weight of the whole stem was calculated by summing the dry weights of all five individual internodes. The target structural stem biomass ranged from 2.78 t ha^{-1} for a 0.7 m tall crop 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} with a lodging return period of 25 years. Root biomass was estimated by first calculating the root plate spread required to withstand the wind induced plant leverage, then using empirical equation $y = 0.038x + 30.2$ from Fig. 6 for 2012-13 data, where the “y” value is the root plate spread and the “x” value is the surface root biomass per plant. The target root biomass ranged from 0.69 t ha^{-1} for a 0.7 m tall crop yielding 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 lodging return period of 25 years.

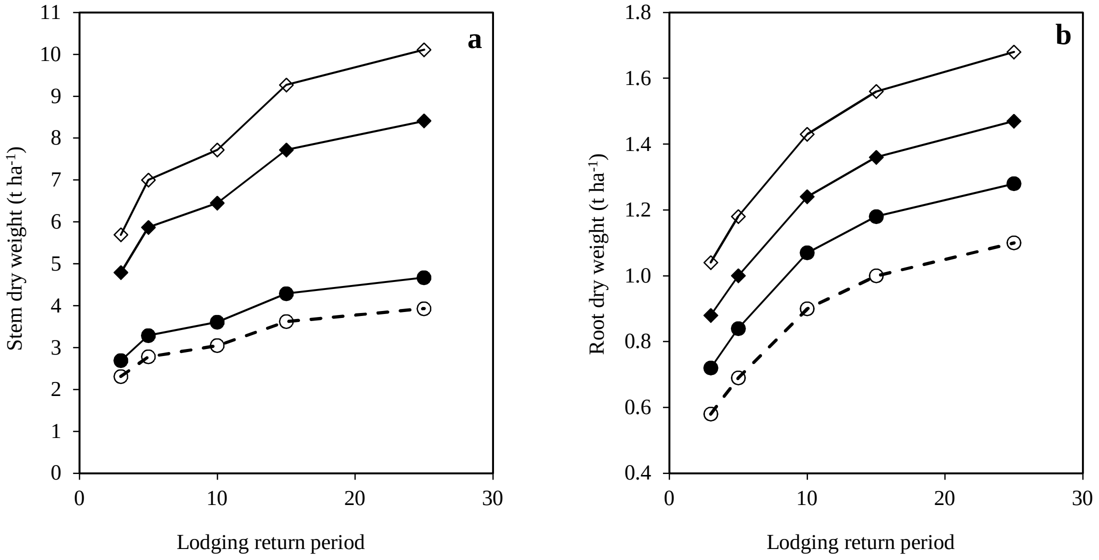

Fig. 7 Stem (a) and root dry weight (b) for a crop yielding 6 t ha^{-1} with a crop height of 1.0 m (♦) and 0.7 m (○), and crop yielding 10 t ha^{-1} with a crop height of 1.0 m (◊) and 0.7 m (●), for different lodging return periods in the NWM environment. Dotted line indicates a NWM wheat crop with current average yield of 6 t ha^{-1} and putative minimum crop height compatible with this yield of 0.7 m

Applicability of the lodging model

The winter wheat lodging model has demonstrated significant accuracy to predict timing and amount of lodging (Berry et al. 2003b). However, its applicability for spring wheat has not been tested. The experiment of 2011 experienced enough natural lodging to test the lodging model developed for spring wheat by comparing the severity of natural lodging against the predicted lodging risk calculated by the model. An index for natural lodging for each cultivar was calculated by summing the percentage of lodged area (recorded once or twice a week during the lodging period) between the first occurrence and harvest. The model predicted lodging susceptibility was calculated by inputting the values of the lodging-associated characters into the model and calculating the mean value of the stem and root failure wind speed which ranged 7.6 to 11.7 m s^{-1}. Lodging occurred during early to mid-grain filling on 35 cultivars whereas 28 were predicted by the model; lodging was absent in 25 genotypes and 12 were predicted by the model. Considering this, from the total of 60 cultivars the model correctly predicted 40 genotypes for either absence or presence of lodging giving a percentage of correct predictions of 67 %. Figure 8 is showing a reasonable correlation between observed and predicted rankings for cultivar lodging resistance.

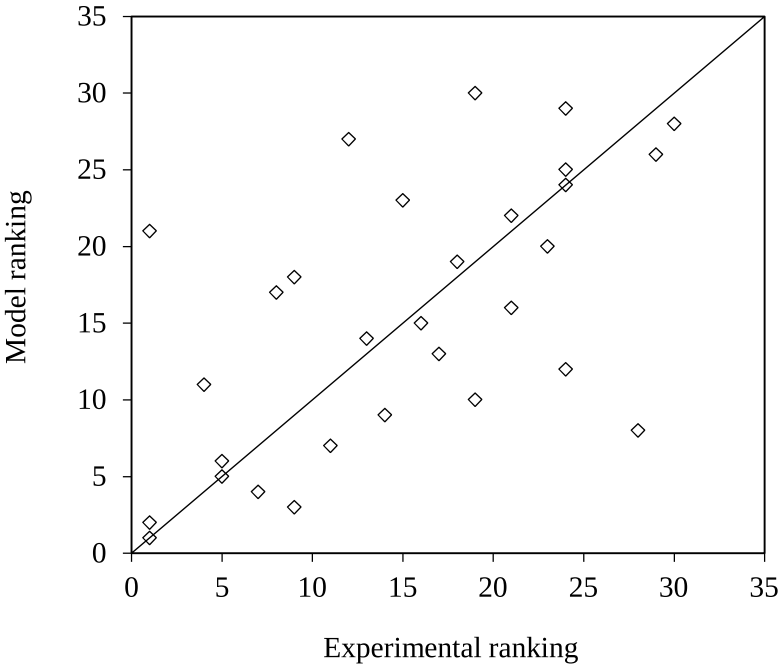

Fig. 8 Predicted and experimental ranking of spring cultivars for lodging susceptibility under NWM environment during 2011. Ranking is in ascending order. (—) 1:1 line. Best fit line, y = 0.60x + 6.52; R^2=0.35 ($P < 0.001$)

Discussion

Comparison of results with published literature

Wind speed analysis for NWM environment has demonstrated that spring wheat growing in these conditions must withstand 22 m s^{-1} and 18 m s^{-1} to resist stem and root lodging, respectively. This indicates that spring wheat will require stronger stems than UK winter wheat (18 m s^{-1} for stem and root lodging risk) (Berry et al. 2007) and similar anchorage strength to support plants with the same height and yield and have lodging only once in 25 years. However, several differences between spring and winter wheat types must also be considered. It has been found that for a height at centre of gravity of 0.5 m spring wheat had a greater natural frequency of 1.5 Hz compared with about 1.0 Hz for winter wheat (Berry et al., 2004). Typical ear area for spring wheat averaged about 19 cm^2 compared with 12 cm^2 for winter wheat with slightly greater yield and similar ears m^{-2}. It is likely that the absence of awns on UK winter wheat explains at least part of this difference. Overall these differences mean that spring wheat will have a greater leverage than winter wheat for crops with the same height, yield and ears m^{-2} (spring wheat = 383 N mm; winter wheat = 297 N mm).

Stem failure moment values for the bottom internode ranged from 134 to 252 N mm (Table 4). These values are higher than the range of the stem failure moment measured in cultivar trials carried out on winter wheat in the UK which ranged from 122 to 230 N mm (Berry et al 2003b; Berry et al 2007). This study has shown a strong relationship between stem strength and structural stem biomass and between anchorage strength and surface root biomass. If there is limited scope to reduce lodging risk by further shortening crops then stem strength and anchorage strength will need to be increased, and this may have a substantial biomass cost that will compete against grain yield formation. A previous study on winter wheat (Berry et al. 2007) estimated that a stem dry weight per unit length of 1.65 mg mm^{-1} was required to achieve a stem strength of 100 N mm. However, the estimated biomass required for stem strength included both structural and water soluble carbohydrate (WSC) and may therefore have over-estimated the amount of structural stem biomass required for stem strength. In the present study, WSC content was not related to the stem strength whereas structural biomass (composed mostly of lignin, cellulose and hemicellulose) was strongly and positively associated with the stem strength. Knapp et al (1987) stated that lodging could be not related to fluctuations in WSC and structural carbohydrates content. On the other hand, Ma (2009) found the wheat gene TaCM (involved in lignin biosynthesis) was associated with stem strength and lodging index and Wiersma et al (2011) found a positive association between lodging resistance and acid detergent lignin (ADL) whilst Wang et al (2012) proposed that cellulose plays an important role in the ability of wheat stems to resist lodging. There is therefore little evidence to suggest that WSC contributes to stem strength. The present study measured that 1.13 mg mm^{-1} of structural biomass is required to achieve a stem strength of 100 N mm. If it is assumed that spring and winter wheat have similar stem biomass/strength properties, then this indicates that the study of Berry et al (2007) may have over-estimated the stem biomass required to achieve specific strength targets by 40 – 50%.

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

Implications of achieving a lodging-proof plant

It has been estimated that to achieve a 1 in 25 year lodging return period for a typical spring wheat crop grown in the NWM environment yielding 6 t ha^{-1} (at 12% moisture) with a height of 0.7 m will require approximately 3.93 t ha^{-1} of structural stem biomass. Unpublished data from experiments described in this study in 2011-13 shows that on average an additional 0.80 t ha^{-1} of biomass is required for the leaf lamina and sheath, and the chaff to grain dry weight ratio of 0.22 (Piñera-Chavez et al., 2016) gives a chaff dry 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 over 6 t ha^{-1} have been observed in NWM (Piñera-Chavez et al., 2016). This ideotype would require a surface root biomass of approximately 1.10 t ha^{-1} which was not been achieved by any cultivar in this study. It therefore appears that for this ideotype it should be possible to achieve stem biomass requirements but not root biomass requirements with current germplasm. The NWM environment can support greater yield than the average 6 t ha^{-1} currently achieved and could be up to 9 t ha^{-1} (Fischer and Edmeades, 2010). It is estimated that cultivars yielding 10 t ha^{-1} (with a height of 0.7 m) will require greater above-ground non-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 root biomass to achieve a lodging return period of 25 years. It should further be recognised that the breeding program at CIMMYT has increased the plant height of wheat to 1.0 m or above in the period of 1966 to 2009 (Aisawi et al. 2015), where the raised bed planting system may favour taller crops better at capturing the light in the gaps between the beds early in the season (Fischer et al. 2005). In the UK, Berry et al (2014) has shown that breeders have not shortened varieties since the 1990s. This indicates that achieving 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 with a 1.0 m tall crop, then the above-ground non-grain biomass requirement increases to 10.1 t ha^{-1} and the surface root biomass to 1.68 t ha^{-1}. These biomass requirements will be very challenging to meet and illustrate that breeders must breed not only for greater total biomass, but also this biomass must be optimised carefully to maximise strength per unit of biomass. Certainly, it will be possible to increase total biomass as shown in the UK (Shearman et al., 2005) and in NWM (Aisawi et al. 2015). Recently, several studies have identified QTLs that could be used to increase both yield and straw biomass (above-ground biomass) in wheat (Berry et al., 2008; Li et al., 2014; Xu et al., 2014). Other cereals such as rice have also shown QTLs related to both yield and straw biomass (Suji et al., 2012). Optimising how the additional dry matter is partitioned to maximise its usefulness will be very important. Targets for improving the efficiency with which non-grain biomass is used include; maximising stem strength per unit of stem biomass, maximising grain weight to ear weight ratio, minimising the production of infertile tillers and achieving high yields with shorter crops. Breeding for wider stems seems to be the most efficient way to increase the stem strength which together with a reduced leverage given by a shorter plant represents a strategic option to minimise structural biomass requirements. Additionally, breeding for more compact ears (unawned) in spring wheat could further reduce this leverage and consequently reducing more the biomass requirements. However, careful must be taken because awned ears have been related to drought and heat resistance (Blum, 1986).

Dry matter harvest indices for these lodging proof ideotypes equate to 0.46 for a 0.7 m tall crop yielding 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 figures are some way below the estimated potential harvest index for wheat of 0.62 (Austin, 1980). Winter 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 0.42 (Berry et al., 2007). However, it is likely that this study over-estimated the stem biomass requirement by including water soluble stem carbohydrate in the stem biomass measurements. If the same relationship between stem failure and structural stem weight observed for this present study for spring wheat is used for winter wheat, and a leaf and leaf sheath biomass of 1.0 t ha^{-1} is included, then this gives a harvest index of 0.49. The relatively high levels of non-grain biomass and low harvest indices that are estimated to result from breeding crops with a lodging return period of 25 years suggest that the high investment in non-grain biomass may compete with yield formation and limit the rate of breeding improvement in grain yield. This potential trade-off arises from the overlapping of the development periods of lodging traits and key yield-determining processes such as floret development and production of water soluble reserves. In fact, Slafer and Rawson (1994) stated that all the processes included from GS30 to GS60 (Zadoks et al., 1974) are considered of major importance for yield construction. Crook et al. (1994) described the development of the lodging characters (stem and root strength) from tillering (GS20) until maturity (GS87) and concluded that these traits cessed develop soon after anthesis (GS65). There may be a net yield benefit from accepting a shorter lodging return period, since the advantage of lower non-grain biomass investment on yield potential may outweigh yield losses from more frequent lodging. If the lodging return period is reduced from 25 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 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 for a 1.0 m tall crop yielding 10 t ha^{-1}.

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

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

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

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

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

Conclusion

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

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Supplementary material

Table S1 The CIMMYT Mexico Core Germplasm Panel (CIMCOG), consisting of 58 *T. aestivum* and two *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/TEMPORALERAM87/ROMO96	2011
22	CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (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	Navojoa 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/SKAUZ//4*BCN/3/2*PASTOR (= Misr#1 in Egypt)	2011
34	OASIS/SKAUZ//4*BCN/3/2*PASTOR/5/FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/7/CAL/NH//H567.71/3/SERI/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	WBLL1*2/KIRITATI (BECARD)	2011, 12, 13
56	WBLL1*2/4/BABAX/LR42//BABAX/3/BABAX/LR42//BABAX	2011, 13
57	WBLL1*2/KURUKU*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES	2011, 12, 13, 14
58	WBLL1*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

*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®)

	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.
Stem characters	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.

781